



An introduction to the European Terrestrial Ecosystem Modelling Activity

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ABSTRACT

The objective of the European Terrestrial Ecosystem Modelling Activity (ETEMA) was to address some of the major challenges in developing generalized models to examine responses of natural and seminatural ecosystems to environmental change at the regional to European scale. The approach described herein was to break down the totality of ecosystem functioning into its key components, each with its characteristic spatial and temporal scales. A conceptual framework was developed describing the configuration of these components as modules within a generalized simulation model. The framework describes the key inputs, outputs and state variables, their spatial and temporal contexts, and information flows between modules. The 'backbone' of the model is a system of nested timing loops corresponding to the disparate time scales at which different ecosystem processes occur. The framework is a theoretical construct into which ecosystem models at levels of complexity ranging

from the very general to the highly detailed can be mapped, and thus provides a guide for development of models for novel, particularly regional-scale, applications. A number of subsystem studies of the major components of ecosystem functioning, i.e. modules of the conceptual framework, are briefly introduced herein. The general aim of the subsystem studies was to identify the key alternative formulations (as opposed to minor variants) and test these against observational data. The various subsystem studies concern planetary boundary layer–ecosystem interactions, ecosystem CO₂ and H₂O fluxes, vegetation physiology and phenology, biogeography and vegetation dynamics, detritus and SOM dynamics, soil moisture and human and natural disturbances and, as individual papers, they complete this special ETEMA issue.

Key words Biogeography, disturbances, ecosystem modelling, fluxes, planetary boundary layer, physiology and phenology, soil organic matter, soil moisture, scale, vegetation dynamics.

INTRODUCTION

Natural and seminatural ecosystems provide many important functions, or 'services', of economic,

cultural and aesthetic value to human society (Costanza *et al.*, 1997). For example, ecosystems provide timber, animal fodder and other materials; process and sequester carbon and nutrients; assimilate wastes; purify water, regulate runoff and moderate floods; build soils and reduce erosion and leaching of soil nutrients; provide recreational opportunities; and act as reservoirs of genetic resources and biodiversity (Intergovernmental Panel on Climate Change, 1998).

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It is now recognized that the integrity of ecosystems and the services they provide are threatened by environmental changes; in particular, increase in the concentration of CO₂ in the atmosphere and associated climate change (Melillo *et al.*, 1996). These changes are likely to affect ecosystems in complex ways. For example, increased CO₂ may increase productivity and water-use efficiency in some plant species, leading to changes in ecosystem function (for example, in net primary productivity; Körner, 1993). Concomitant changes in temperature and rainfall resulting from increased greenhouse gas forcing may accentuate, or conversely mitigate, the direct CO₂ effect on ecosystem function, both through direct effects on photosynthesis and respiration rates (Körner, 1993) and changes in growing season and phenology (Kramer, 1995). These factors are likely to affect species differentially, leading to changes in competitive balance between species and, ultimately, in ecosystem composition and structure, which would have further feedbacks on function (Bazzaz & Carlson, 1984; Stirling *et al.*, 1997; Catovsky & Bazzaz, 1999). Rapidly shifting climatic zones may also leave some species populations 'stranded' beyond their present-day climatic range limits, where they may suffer reduced vitality and, eventually, local extinction (Sykes & Prentice, 1996; Sykes *et al.*, 1996). Changes in land-use patterns may also be expected, as humans respond, for example, to shifts in the areas most suitable for certain types of agriculture or forestry (Beniston *et al.*, 1998).

European ecosystems may be particularly vulnerable in the face of these changes: natural ecosystems tend to be highly fragmented, confined mainly to poorer soils and upland areas. Lowlands and areas with richer soils, which are occupied mainly by agriculture and intensive forestry, would represent barriers that inhibit migration of many species as their optimal ranges shift (Beniston *et al.*, 1998). Centuries of management has probably left many seminatural ecosystems, particularly forests, out of equilibrium with respect to their natural composition and structure, and this may limit their resilience in the face of perturbations of the climate regime (Kienast *et al.*, 1996; Lindner *et al.*, 1997).

There are large uncertainties associated with the factors influencing ecosystem structure and function and their evolution under changing environments (Melillo *et al.*, 1996). To plan for

such an uncertain future it is important to develop a predictive understanding of how ecosystems respond to changes in their key 'driving' parameters: climate, radiation, atmospheric and soil chemistry, natural disturbance regimes and land management. Some progress has already been made at the global scale: equilibrium biosphere models and more recently developed dynamic global ecosystem models (DGVMS) are able to reproduce the potential natural vegetation of the earth, and broad-scale patterns of carbon exchange, runoff, biomass and leaf area index, at a level of precision acceptable for characterizing global-scale responses to climate change (e.g. Neilson *et al.*, 1998; Kucharik *et al.*, 2000; Cramer *et al.*, 2001). At scales ranging from the region (*c.* 10–100 km) to a small continent such as Europe, however, there is greater uncertainty, as simplifying assumptions of homogeneity (for example, in topography and vegetation height), can no longer be made without a critical loss of resolution (see, e.g. Friend, 2001; Woodward & Lomas, 2001).

To be useful for regional-scale impact assessment and planning, models must have the potential to utilize driving data, and generate predictions, on finer spatial grids. Regional users may also demand predictions that are more detailed in other respects; for example, that characterize vegetation by the major species present rather than generalized plant functional types. In general, this implies that regional models must include more detail for some processes (e.g. plant competition for light and other resources; see Smith *et al.*, 2001), while empirical components (typically simple constants) are replaced with more or less mechanistic formulations of the processes they represent (e.g. modelling hydrological flows between areas of differential topography, in place of a grid-cell average value for soil water).

Different ecosystem processes operate on different spatial scales and at widely different rates. As models grow to incorporate explicit formulations of a larger number of key processes, technical challenges arise in linking their different characteristic spatial and temporal scales. Not all of these challenges have been addressed before, as ecosystem models in the past have characteristically focused on one set of processes, while representing other processes much more crudely, thus avoiding the need to transcend different scales in their operation (see below).

The European Terrestrial Ecosystem Modelling Activity (ETEMA) was developed to address some of the major challenges in developing generalized models to examine responses of natural and seminatural ecosystems to environmental change at the regional to European scale. The approach was to break down the totality of ecosystem functioning into its key components, each with its characteristic spatial and temporal scales. A conceptual framework was developed describing the configuration of these components as modules within a generalized simulation model. The framework describes the key inputs, outputs and state variables, their spatial and temporal contexts and information flows between modules. The 'backbone' of the model is a system of nested timing loops corresponding to the disparate time scales at which different ecosystem processes occur. The framework is a theoretical construct into which ecosystem models at levels of complexity ranging from the very general (such as existing dynamic global models) to the highly detailed can be mapped, and thus provides a guide for development of models for novel, particularly regional-scale, applications.

This conceptual framework is described in this paper. Subsequent papers in this special issue each concern a subsystem study of one of the major components of ecosystem functioning, i.e. one module of the conceptual framework. For most subsystems, a number of alternative plausible formulations exist and have been used in various models. The general aim of the subsystem studies was to identify the key alternative formulations (as opposed to minor variants) and test these against observational data. Outcomes of the studies range from outright rejection of certain approaches, to recommendation of different approaches for addressing different classes of questions (for example, at different scales). The subsystem studies and their outcomes are summarized briefly in the present paper.

THE ETEMA MODELLING FRAMEWORK

Spatial scales

Ecosystem processes take place at a wide range of different scales, ranging from a few square centimetres (the scale at which, for example,

exchange of water vapour and CO₂ between the leaf surface and the atmosphere is controlled) up to hundreds of square kilometres (e.g. at which bioclimatic limits on the distributions of particular vegetation types may be resolved). Traditionally, ecosystem models have treated variation at one scale explicitly, incorporating smaller scales implicitly within assumptions in the formulations of various processes, while 'scaling-up' to larger scales, usually by simple averaging or addition.

For example, biosphere models and DGVMs that have been used to characterize vegetation patterns and ecosystem cycling at continental to global scales (e.g. VEMAP Members, 1995; Neilson *et al.*, 1998; Kucharik *et al.*, 2000; Cramer *et al.*, 2001) generally resolve variation at the scale of a grid-cell of 0.5 latitude and longitude degrees on a side. Variation within grid cells is accommodated by averaging assumptions incorporated in the formulations of the processes modelled. Gap models of forest stand dynamics generally have a patch, defined as the area of influence of a single adult tree on its neighbours (Prentice *et al.*, 1993), as the basic spatial unit. This enables vegetation dynamic processes of establishment, mortality and competition between individuals, as well as certain types of disturbances, to be treated mechanistically in such models. The patches usually represent independent 'random samples' of the stand (or regional) vegetation, whose attributes can be averaged to characterize the regional vegetation (see Smith *et al.*, 2001).

It may not always be feasible to represent the finest spatial scales explicitly, due to the high computational expense of fine resolution models, and because of increased difficulties in analysing coupled model behaviour. To minimize complexity, while maintaining sufficient flexibility and precision for regional-scale applications, we adopt an approach in which two spatial scale levels, and links between them, are explicitly defined. We distinguish 'macro cells', *c.* 10–50 km on a side and geographically referenced; and 'micro cells' of which one or many may be contained within each macro cell.

Macro cells would normally adjoin one another on a regular grid spanning the entire domain to be modelled. Cells may differ from each other in terms of statistical distributions (or, in the simplest case, means) of macroclimatic

parameters and soils, and in the basic nature of the landscapes within them (lowlands, mountains, etc.). While the heterogeneity in the primary physical environment is prescribed for each macro cell, ecosystem attributes (e.g. PFT composition, stage following disturbance or harvesting) and ecosystem-driven features of the environment (e.g. soil moisture levels) may vary during simulation. This heterogeneity is accommodated by the micro cells nested in each macro cell. Ecosystem processes would normally be simulated independently for each macro cell, but cells could also be connected by horizontal fluxes of water (as runoff) or propagules (for modelling vegetation migration).

Micro cells are the basic units for modelling of 'vertical' fluxes of water and carbon between vegetation and the atmosphere, and water, carbon and nitrogen between vegetation and soils. Depending on the level of model complexity chosen for a particular application, there may be one or many micro cells in each macro cell, they may be spatially referenced or not, and may vary in conceptual size from a point, to a patch, to the area of the entire macro cell.

Temporal scales and key modules

Different ecosystem processes also vary in their characteristic time-scales. We assume a model configuration in which canopy-atmosphere exchange and planetary boundary layer dynamics are modelled mechanistically, driven by input data derived from weather-generator-produced daily averages for air temperature, precipitation and other 'weather' variables, with prescribed assumptions as to the shape of the diurnal cycle of these variables. State variables associated with these processes then need to be updated on a simulation time-step of one or at most a few hours, which we term the 'fast' time-step. Canopy exchange is closely tied to soil moisture dynamics (through the coupling of photosynthesis and soil-plant water exchange via canopy conductance), which should therefore also be updated on the fast time-step. These processes, together with computations of soil temperature and heat dynamics, comprise three modules of the conceptual framework that are called consecutively once every time-step within the innermost timing loop of the framework (Fig. 1).

Phenological processes and whole-plant aspects of plant physiology (such as allocation of assimilated carbon) tend to be modulated by seasonal signals (changes in temperature and daylength and, secondarily, in nutrient and water availability), and may therefore be modelled at a temporal resolution of between a day and one or a few months. This is also the appropriate time-scale for modelling of litter decomposition and soil organic matter (SOM) dynamics and for disturbances (such as fire or wind-throw) that follow a seasonal incidence probability curve. These processes comprise the three modules of the 'intermediate' timing loop of the framework.

Vegetation dynamics (defined as changes in the relative and absolute abundance of different vegetation components, through establishment of new individuals, mortality and migration) are driven by plant life-cycles, which are influenced both by natural conditions (the physical environment and interactions with other organisms) and, potentially, by human activities, such as planting and harvesting of forest plantations and crops. We assert these processes into two modules — one comprising formulations of the natural components of vegetation dynamics; the other, human land use. These modules are called within the outermost loop of the framework, on a 'slow' time-step of 1 year or more.

State variables — links between modules

The key modules of the framework are linked by state variables, i.e. stored and labelled data associated with a particular module that are (potentially) updated each time the module is called and available for other modules to query as required. The state variables thus provide links between the modules of the framework, as well as potential output from the model. The main links are shown in Fig. 2.

Potential temperature, wind speed, air humidity, air pressure, incoming shortwave and longwave radiation, precipitation, atmospheric CO₂ concentration

These climate/weather drivers are potential inputs to the planetary boundary layer (PBL) module, which is called by the framework every fast time step to predict the height of, and conditions within, the PBL, based on driving climate and PBL state at the previous time step. States of

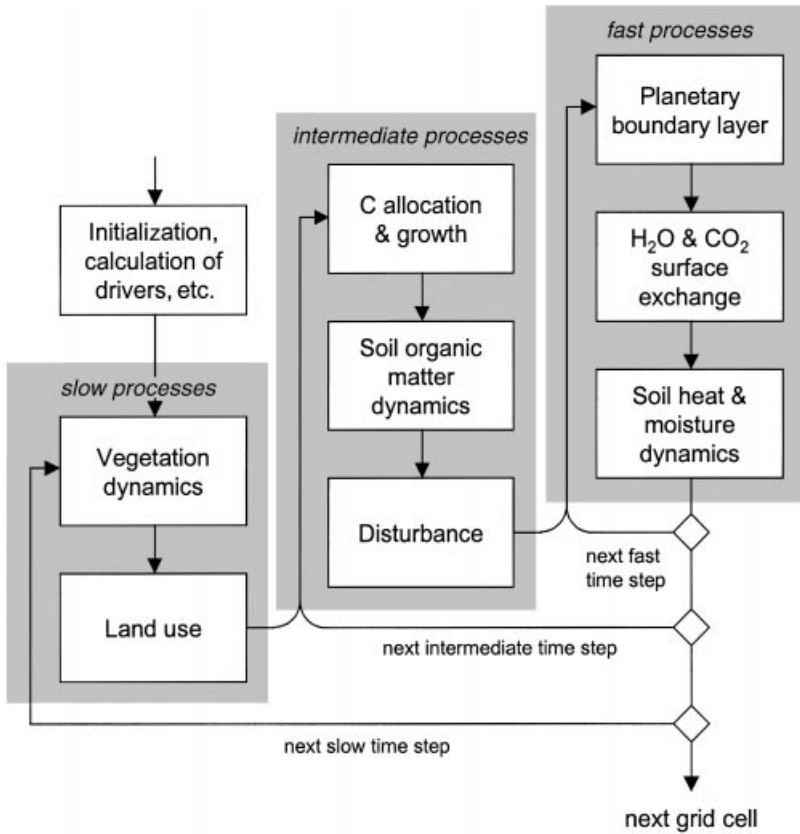


Fig. 1 Execution flow diagram for the conceptual ecosystem modelling framework, showing the major process modules and the order in which they would be called from within three nested timing loops implementing, respectively, a slow time step (c. 1 year); intermediate time step (c. 1 day–3 months); and fast time step (c. 1–3 h).

the same variables within the PBL are passed on to the H₂O and CO₂ surface exchange module, where they are used as drivers for the coupled processes of photosynthesis and canopy conductance of water vapour and CO₂, and for autotrophic respiration. Downward radiation, air temperature within the PBL and precipitation may also constitute inputs to modelling of soil heat and moisture dynamics.

Heat and momentum, outgoing shortwave and longwave radiation from vegetation, vegetation–atmosphere CO₂ and water vapour fluxes

States of these variables are predicted by the H₂O and CO₂ surface exchange model each fast time step and comprise a feedback to the PBL. Water vapour flux (i.e. evapotranspiration) is

simultaneously coupled to the soil heat and moisture dynamics module, to implement a canopy conductance feedback on soil moisture status.

Soil moisture

This state variable is updated within the soil heat and moisture dynamics module, and provides a potential limitation on vegetation canopy conductance, as well as influencing heterotrophic respiration (SOM dynamics module) and relative allocation of assimilated carbon to roots (carbon allocation and growth module).

Soil temperature

Predicted by soil heat and moisture dynamics module, soil temperature influences heterotrophic respiration (SOM dynamics module) and respiration

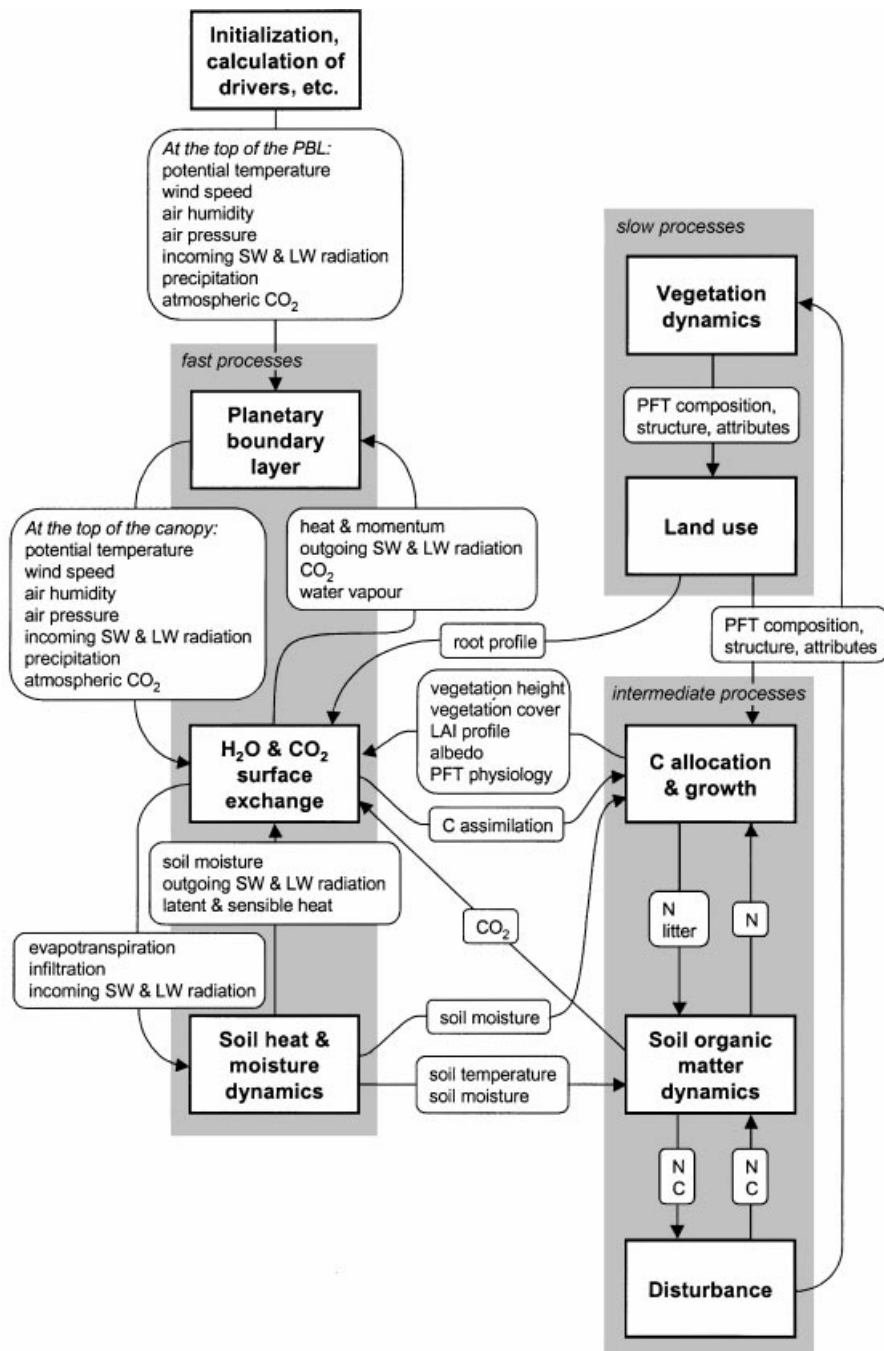


Fig. 2 Major process modules of the framework showing data links between modules (see text).

by plant roots (H_2O and CO_2 surface exchange module).

Outgoing shortwave and longwave radiation from soil surfaces, latent and sensible heat

Outputs from modelling of soil heat and moisture that may be passed to the H_2O and CO_2 surface exchange module or directly to the PBL.

Carbon assimilation

Assimilated carbon is predicted by the H_2O and CO_2 surface exchange module and converted to new biomass on the intermediate time step within the C allocation and growth module.

Heterotrophic respiration

CO_2 released by heterotrophic respiration (SOM dynamics module) is passed to the H_2O and CO_2 surface exchange module, or directly to the PBL.

Litter

Litter production due to biomass turnover (C allocation and growth module) or biomass destruction by disturbance (disturbance module) constitutes input to the SOM dynamics module. Litter inputs augment 'slow' and 'fast' soil carbon pools (or alternatively, provide new cohorts of soil organic matter) and may also (via litter C : N ratio) influence soil available nitrogen status.

Soil available nitrogen

Potentially influences relative allocation to roots or other biomass compartments as well as tissue C : N ratios in the C allocation and growth module.

Vegetation height, cover, LAI profile, albedo

Variables updated on the intermediate time step by the C allocation and growth module and used as parameters to photosynthesis and other calculations within the H_2O and CO_2 surface exchange module.

Vegetation composition and structure

Vegetation composition in terms of plant functional types (PFTs) is updated by the vegetation dynamics module (for 'natural' succession) and the land use module (anthropogenic controls on dynamics, including planting, harvesting and silvicultural treatment). PFT composition and vegetation attributes, which will generally be derived from prescribed physiological, phenological

and population dynamic attributes of the component PFTs, are required as input to the carbon allocation and growth module and the H_2O and CO_2 surface exchange module.

SUBSYSTEM STUDIES

Subsystem studies, each of which concerns a subsystem study of one of the major components of ecosystem functioning, i.e. one module of the conceptual framework, form the major part of this special issue. In this introductory paper they are described only briefly.

The aim in these studies was to compare a range of feasible model representations of each class of process entailed by the subsystem concerned. By comparing the performance of different model formulations to data from real world ecosystems, the relative merits of the various possible formulations could be assessed objectively. In some cases, it was expected that different formulations might be appropriate under different sets of driving conditions, at different scales, or to address different questions.

Planetary boundary layer–ecosystem interactions

Ecosystem–planetary boundary layer interactions provide the vertical link between the moisture content of the PBL in which ecosystems are situated, and the free atmosphere above. Modelling PBL processes is important in the context of large-scale ecosystem modelling because stomatal conductance and evapotranspiration are functions of the moisture content of the PBL while, in turn, the moisture content of the PBL is influenced strongly by evapotranspiration from ecosystems (Jarvis & McNaughton, 1986; Troen & Mahrt, 1986; de Bruin & Jacobs, 1989; Jacobs & de Bruin, 1992). The PBL integrates evapotranspiration and other fluxes (e.g. of CO_2) at a regional scale, so that adjacent ecosystems within a region are connected through the PBL. Because the state of a single patch of vegetation within a heterogeneous area will not be expected to change independently from other patches in the same region, neglecting PBL feedback may result in severe inaccuracies in predicting ecosystem responses to changes in atmospheric conditions, particularly the effects of warming on ecosystems

where water is or becomes limiting (Eamus, 1991; McNaughton & Jarvis, 1991; Friend & Cox, 1995).

To date, regional- to global-scale ecosystem models have lacked an explicit PBL, incorporating instead a general parameterization of the effect of atmospheric humidity on evapotranspiration (e.g. Monteith, 1995). One reason for this is the incongruity between the characteristic scales of processes feeding into the PBL (differential evapotranspiration from vegetation patches of varying composition and structure) and the mixing within the PBL, which occurs at scales of > 10 km. Few models to date have included patches and regions as distinct spatial units.

The model presented by Woodward & Lomas (2001) is the first detailed formulation of PBL function developed explicitly as a component of a coupled ecosystem model. Separate submodels apply to the subregional < 10 km scale, typically characterized by a disorganized heterogeneity of vegetation patch types, and the > 10 km scale at which discrete boundaries between vegetation types (organized heterogeneity) may be seen. Fluxes from separate patches of vegetation in a disorganized heterogeneity are mixed mainly in the bottom 100 m surface layer of the PBL and may simply be averaged, weighted by areal cover, to give the approximate overall flux entering the mesoscale circulation in the upper 1–2 km of the PBL. At the broader scale, it is necessary to model explicitly entrainment of the averaged fluxes from the surface layer into the PBL proper, as well as the diurnal growth and collapse of the PBL ceiling. The PBL model is linked to the coupled framework by vegetation structure, updated on a timestep of *c.* 1 month–1 year, and fluxes of H₂O and CO₂, updated on a fast timestep of ≤ 0.5 h. Its fast-timestep predictions of humidity and CO₂ concentration at the canopy surface in turn drive the photosynthesis module of the coupled model.

The PBL model is successful in reproducing observations of wind speed changes across heterogeneous canopies, and observations and previous simulations of PBL height evolution above landscapes dominated by different vegetation types (Woodward & Lomas, 2001). Model predictions of humidity profiles at different times of the day are also consistent with expectation based on theory and observations.

Vegetation physiology and phenology

The capacity of the 'fast' ecosystem processes to respond to the environment is dependent on vegetation physiology and phenology. These attributes link the structure and function of the vegetation. The physiology of the vegetation is taken to consist of properties that remain fixed (over the year, or at least over periods of days to weeks) while the ecosystem CO₂ and H₂O fluxes vary. Examples include foliage area profile, foliage nitrogen content, respiring biomass and rooting depth. These system state variables must be determined from the vegetation composition and structure, including phenological status. In turn they modify the calculations of the short-term fluxes.

The phenology of the vegetation depends on the plant types that are present, and the 'rules' that determine how these plant types regulate budburst and abscission as a function of environmental variables. The nature of these rules has become an active area of experimental research since it has been realized that some of the most direct effects of climate change, especially winter warming, as expected at high latitudes, are likely to be mediated by phenology. Possible effects of warming include 'paradoxical' responses such as increased frost damage due to early budburst (Cannell & Smith, 1986) and range reductions of species with high chilling requirements (Sykes *et al.*, 1996). Quantitative experimental and observational data are now available describing the phenological behaviour of many evergreen and cold-deciduous European woody species (e.g. Murray *et al.*, 1989). Drought-deciduous phenology is also present in Mediterranean ecosystems and important in subtropical ecosystems.

A key assumption made in many area-averaging models of vegetation is that leaf nitrogen content (which is correlated with, and mostly contained within, the carboxylation enzyme rubisco) is regulated by plants so as to optimize net carbon assimilation, i.e. falling with canopy depth in linear response to time-mean PAR. This is a convenient assumption, because it allows entire vegetation canopies to be treated as a 'big leaf', characterized by canopy-average values for the parameters governing carbon assimilation and transpiration: vertical profiles of leaf N and light attenuation through the canopy can be ignored.

The big leaf model has, however, been criticized recently. First, measurements of canopy profiles of nitrogen do not clearly match the expected optimum distribution (Kull & Niinemets, 1998). Secondly, within-leaf heterogeneity may give rise to different limiting rates of photosynthesis, and therefore different nitrogen optima, in different regions of the same leaf. Results of modelling taking account of such variable rates have been shown to provide a closer match to observations of whole-canopy photosynthesis (Badeck, 1995; Kull & Kruijt, 1998). Friend (2001) systematically tests the validity of the big leaf assumption by simulating canopy-level photosynthesis with, on one hand, a traditional biochemical model assuming a canopy-average photosynthetic response, and on the other hand a model taking account of within-leaf heterogeneity in photosynthetic behaviour. The models are configured identically with respect to their common parameters. The more detailed model is found to yield significantly different (higher) rates of net photosynthesis. Predictions are also affected by adding a declining vertical profile of leaf N, or an observed, as opposed to uniform, vertical distribution of leaf chlorophyll, as well as by taking account of sun (direct PAR) and shade (diffuse PAR) regions within the canopy.

This analysis tends to reject the general but oversimplistic big leaf approach, and suggests that more detailed physiology may be needed to obtain accurate predictions of canopy-level photosynthesis from a dynamic vegetation model, such as that provided by the ETEMA framework.

Biogeography and vegetation dynamics

The processes that determine what plant types and species are present at a certain location, and in what abundance, operate on time scales up to decades and even centuries. Biogeographic distributions of many broadly defined functional groups of plants (PFTs, e.g. broad-leaved evergreen woody plants, boreal evergreen conifers, temperate deciduous trees, C4 grasses) have been shown to correspond to climatic extremes such as minimum winter temperatures and summer drought (Woodward, 1987; Sykes *et al.*, 1996). Underlying these limits are ecophysiological constraints on plant function. Ecophysiological constraints on broadly defined plant types formed

the basis of the first generation of global biogeography models (e.g. Prentice *et al.*, 1992). While current state-of-the-art models include a considerable amount of plant physiology, some bioclimatic limits on PFT distributions are still necessary, to account for physiological constraints that are still poorly understood, impractical to model, or for which measurements with which to parameterize the underlying processes are not available.

Apart from physiological limits, constraints on migration rates might conceivably delimit distributions of some PFTs, particularly under the transient conditions associated with a rapid climate change. Palaeoecological data are available to help in describing the large-scale spatial process of migration of species, although in reality the present situation is very different. Landscapes are extensively fragmented through land-use and on the other hand humans are capable of spreading species over wide areas, accidentally or deliberately. Nevertheless, modelling of large-scale migrations taking into account fragmentation of habitats is possible within the ETEMA framework, for example by reducing the range of possible outcomes by analysing specific regions and vegetation types (Pitelka *et al.*, 1997).

Within the ecophysiological limits of species/PFT distributions, and given the availability of propagules, vegetation composition is determined by demographic and competitive processes. Given a set of PFTs physiologically adapted to ambient climate conditions, the processes of growth, regeneration, mortality and competition for light, water and nutrients determine the time-evolution of species populations and their age- and size-structure. These processes are ultimately driven by NPP and allocation strategies (e.g. shade-tolerant vs. shade-intolerant syndromes) of different plant types. Recent developments in modelling of vegetation at regional to global scales have led to simplified parameterizations of competition among PFTs, based on areal averages of plant structure and growth (e.g. Foley *et al.*, 1996; Sitch, 2000). Area-averaging has the advantage that the stochastic processes operating at the neighbourhood scale (at which competition truly occurs), as well as among-individual variation in structure and performance, can be ignored, greatly improving computational efficiency. However, the validity of the area-based approach, particularly at finer spatial

scales and for more narrowly defined PFTs and species, has not previously been assessed.

Smith *et al.* (2001) compare predictions of two models of vegetation development, configured identically with respect to core physiological processes and cycling of carbon and water, but differing in their formulations of the processes governing vegetation dynamics (establishment, mortality and competition for light and water). For a range of locations spanning the present-day climate variation within Europe, both models were able to predict the correct equilibrium potential vegetation in terms of the qualitative composition of major plant functional types. However, the models differed in the relative amounts of different PFTs predicted in some climates, particularly those characterized by pronounced seasonal water deficits, or in which codominance by evergreen and deciduous PFTs is possible. In such climates, the individual-based model, with its essentially 'mechanistic' representation of proximal plant interactions, gave better predictions than the more parameterized area-based model. This analysis suggests that a relatively explicit approach to modelling of vegetation dynamics may be a necessary trade-off in ecosystem modelling at the regional to continental-scale.

Detritus and SOM dynamics

Detritus and SOM dynamics influence vegetation dynamics by regulating the supply of mineral N to plants, and ecosystem CO₂ fluxes, by determining the amount of carbon in different SOM fractions (Schimel *et al.*, 1994). The dynamics of microbial decomposition and transformation of nonliving plant material involves a wide range of time scales from subannual changes in detrital inputs (related to vegetation physiology and phenology) and N mineralization rates, to century- to millennium-scale changes in the slowest carbon pools. Here we exclude from consideration only the slowest of these processes, i.e. we are not concerned with the 'passive' carbon pools or peat accumulation, but we are concerned with processes operating at time scales up to and including the time scale of vegetation dynamics.

Gains and losses of N to the ecosystem are also important on decade to century time scales. N is lost by leaching, but European ecosystems have received large doses of N from the atmosphere

in recent years. These anthropogenic sources of N may or may not be influencing vegetation composition and productivity (e.g. Schindler & Bayley, 1993; Binkley & Högberg, 1997; Jenkinson *et al.*, 1999; Nadelhoffer *et al.*, 1999).

While the other subsystem elements considered by ETEMA had not been subjected previously to a rigorous validation of different approaches, in the case of soil organic matter dynamics, a comprehensive intercomparison of different approaches and their performance in comparison to observational data was carried out by SOMNET (Smith *et al.*, 1997). This study led to the conclusion that the CENTURY formalism for below-ground C–N coupling (Parton *et al.*, 1987, 1988; 1993; 1994) remains widely applicable to both natural and agricultural soils. The CENTURY approach, however, is limited by an absence of temporal structure: cohorts of litter in different stages of decay are not traced. For an ecosystem model such as ETEMA, with litter inputs from dynamically varying vegetation, the more precise modelling of carbon dynamics offered by a cohort-based approach is a highly desirable feature. The SOMKO model, developed by Gignoux *et al.* (2001) combines a highly mechanistic representation of the fundamental biological and physical processes driving soil carbon and nitrogen dynamics with cohort structure. The model is successful in mimicking single-cohort carbon and nitrogen dynamics from 'litter bag' experiments, and exhibits reasonable long-term responses to a simulated climate change.

Human and natural disturbances

Besides factors that directly influence plant physiology and phenology, there are physical agents that cause change in vegetation structure by mechanical damage and/or removal of plant tissues. Disturbances are 'normal' elements of ecosystem dynamics, yet have often been ignored or treated simplistically in ecosystem models. It is essential that the nature of the local disturbance regime is considered, both for a steady state description of a 'mature' ecosystem, and for the assessment of transient change due to changing climate, CO₂ or land use.

Vegetation dynamics are affected directly by both human and natural disturbances by removal of biomass in forest harvest, grazing, windstorms,

avalanches and fires. Contemporary ecologists recognize that even natural ecosystems are, or were, typically a mosaic of patches of different age (i.e. time since the last major disturbance) (Pickett & White, 1985; Veblen, 1992). In semi-natural ecosystems the biomass removal has been co-opted by humans. We thus treat these two aspects of disturbance together.

Major disturbances considered for the ETEMA framework, as being of importance in a European context, are:

- fire (in Mediterranean, temperate and boreal ecosystems);
- breakage by wind (in temperate and boreal forests);
- abrasion by wind and ice (in boreal and tundra ecosystems); and
- effect of herbivores and fungal pathogens (in all ecosystems).

Thonicke *et al.* (2001) address disturbance through fire using a generalized fire module. Fire is modelled using a statistically based fire history approach and a process-based estimation of fire conditions related to soil moisture. The probability of fire occurring is dependent on fuel load and litter moisture, both of which are related to climate and the vegetation of the site. Fire effects are driven by the length of the fire season and the different sensitivities of the different plant functional types to fire. Simulations show that the module can be used to predict fire regimes in many ecosystems. In regions where modelled results do not agree with observations this can be related to processes not included in the model, such as permafrost or edaphic conditions, or to the role of humans with regard to fire management and land use.

CONCLUSIONS

The papers presented in this special issue summarize the work of ETEMA, excluding the completed pilot study of the application of the coupled model on a spatially extensive basis across Europe (available from the authors). The ETEMA project defined a configuration of an integrated framework for modelling the structure and function of ecosystems from the patch, to regional, to continental scale, and has completed a comparative analysis of modelling approaches for various subsystems within this framework.

Through the subsystem studies, progress has been made towards an improved parameterization of the physical, chemical and biological processes underlying ecosystem dynamics and their consequences at the relevant temporal and spatial scales for modelling responses to environmental change.

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