Ann. Sci. For. (1998) 55, 1–11

Original article

Variation in forest gas exchange at landscape to continental scales

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(Received 18 August 1997; accepted 20 October 1997)

Abstract – The European Community project EUROFLUX has established the first network for monitoring and comparing gas exchange of forest ecosystems via eddy covariance techniques at the continental scale, applying both standardized instrumentation and software. The EUROFLUX workshop entitled 'Water Flux Regulation in Forest Stands' reviewed at the start of the project our current understanding of water relations and water balances in European forests. Recent studies of transpiration via sapflow monitoring methods were highlighted and the view of water flux regulation that they provide was examined. Studies of sapflow are being carried out at EUROFLUX sites together with above canopy flux measurements in order to characterize function of the tree canopy compartment. Sapflow studies at additional European sites extend the environmental gradients along which water fluxes are being observed, e.g. by including forests of riparian zones and of high elevation. Achieving an understanding of forest gas exchange response and forest acclimation potential along climate gradients, and especially in response to environmental stresses at the extreme of the gradients, is essential for integrating information on fluxes and biogeochemistry at landscape, regional and continental scales. (© Inra/Elsevier, Paris.)

forest gas exchange / landscape models / global models / heterogeneity / scaling

Résumé – **Variations des échanges gazeux des forêts de l'échelle locale à l'échelle continentale.** Le projet européen Euroflux a mis en place le premier réseau de mesure et de comparaison des échanges gazeux au-dessus des écosystèmes forestiers à l'échelle continentale, au moyen de la méthode des corrélations turbulentes, en utilisant une instrumentation et des procédures

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de traitement standardisées. L'atelier de travail Euroflux intitulé « Régulation des flux hydriques dans les peuplements forestiers » a évalué au départ du projet les connaissances actuelles sur les relations hydriques et les bilans hydriques dans les forêts européennes. Les études récentes de la transpiration des arbres via les techniques de mesure du flux de sève brute ont été mises en avant, et les résultats concernant la régulation des flux hydriques ont été examinés. Dans les différents sites Euroflux, des mesures de flux de sève sont mises en œuvre parallèlement à la mesure des flux au-dessus des couverts, dans le but de caractériser le fonctionnement du compartiment foliaire des arbres. Des mesures de flux de sève réalisées dans des sites européens additionnels accroissent l'étendue du gradient d'observations des flux hydriques, en incluant par exemple des forêts alluviales et d'altitude. Parvenir à une meilleurs compréhension des échanges gazeux par les forêts, et de leur acclimatation potentielle le long des gradients climatiques, et notamment de leur réponse aux contraintes en situations extrêmes, est essentiel pour pouvoir faire la synthèse des informations sur les flux et sur la biogéochimie aux échelles locale, régionale et continentale.

échanges gazeux des forêts / modèles régionaux / modèles globaux / hétérogénéités / changement d'échelle

1. CO-ORDINATED FOREST GAS EXCHANGE STUDIES AND CURRENT RESEARCH TRENDS

The exchange of water vapor, CO_2 and other gaseous materials between the atmosphere and forest ecosystems is affected by the successional stage of the vegetation [1, 32], the stage of canopy closure, and by growth activity as related to site quality or influenced by atmospheric nitrogen deposition [20, 29, 38]. Additionally, both drought and cold temperature-induced limitations on structure, physiology, phenology and nutrition limit forest exchange capacities [18, 37, 39]. Given that climate model simulations are sensitive to vegetation effects on evapotranspiration (ET - [12, 27]), that vegetation function is strongly influenced by increases in atmospheric CO_2 concentration at sites with limiting water and nutrient availability [7, 24, 33], and that the structure of regional vegetation mosaics is being modified by changing frequencies in natural and anthropogenic disturbance regimes [49], heterogeneity as well as shifts in forest ecosystem function along landscape, regional and continental scale gradients must be better understood. Information on shifts in process regulation must be used to improve the manner in which vegetation/atmosphere exchanges and their feedbacks are parameterized in both global circulation models (GCMs) and models for regional and landscape assessments.

Surface exchange varies due to the manner in which specific vegetation development modifies 1) the interception of precipitation and storage of water in the canopy, 2) surface roughness and microclimate profiles, 3) overstory and understory stomatal conductance, and 4) soil water extraction and coupling to soil water stores [4, 9, 19, 40]. GCMs have purported to reasonably represent these processes at the grid square scale (approximately 50 × 50 km). To date, however, model parameterization has been based on stand level studies or relatively local aircraft measurements, which are assumed to apply homogeneously at larger scales. Due to the ubiquitous influence of man on land-use in all parts of the globe [45], the need for dynamic vegetation models that evaluate the vegetation mosaic and, thus, achieve a reasonable representation of the heterogeneity in vegetation/atmosphere exchange and a basis for translating fluxes and balances into currencies relevant to human concerns is recognized [26, 45, 49].

In this new generation of global, regional and landscape models, parameterization of ecosystem function must be derived either from remote sensing [21, 28, 36] or for global models by upscaling and simplifying landscape vegetation dynamics to represent corresponding processes at grid square scales [50]. Both research efforts focus attention on the understanding of aggregation or process integration within real landscapes. The analysis of ecosystem energy exchange processes along landscape and regional scale gradients is extremely important, since such studies are carried out at the largest scale utilized to date for 'ground truth' verification of ecosystem-related concepts [14, 30, 31, 42]. Thus, landscape and regional studies provide a solid basis for formulating ecosystem models for application at large scales. Sound ecosystem models at landscape and regional scales provide a link between land-use change and socio-economic problems [45], will aid resource management [6, 41], and allow us to test the assumptions of global models.

Recent advances in measurement technologies now permit long-term observations of water and carbon dioxide exchange of forest ecosystems [2, 16, 17]. The European Community funded research project EUROFLUX has established the first measurement network for monitoring and comparing gas exchange of forest ecosystems at the continental scale, using standardized instrumentation and software. The data base now being assembled and to be complemented from a world-wide flux measurement network promoted by the IGBP core project BAHC provides for two imperative needs of ecosystem modellers and resource managers *(figure 1)*. Viewed from a global perspective, a well-distributed network of flux sites will allow comparisons with current ET calculated within GCMs along continental climate gradients. From landscape and regional perspectives, comparative analysis and modelling of the repeated observations within stands of *Picea abies*, *Pinus sylvestris*, *Fagus sylvatica*, and *Quercus ilex (table I)* will help formulate hypotheses about the acclimation potential of major woody vegetation elements along regional and continental environmental gradients. Studies at additional European sites (some of which are described in the contributions to this issue) can be referenced to the EUROFLUX network, enriching the spectrum and value of both sets of investigations. The workshop 'Water Flux Regulation in Forest Stands' established new contacts between EUROFLUX research groups and others involved in forest water balance studies.

The dual potentials for use of EUROFLUX data *(figure 1)* suggests that vegetation/atmosphere exchange models (SVATs as described by Lee et al. [19] and Dolman [10]) should satisfy one of two separate sets of criteria, i.e. should function according to technical restrictions and should be designed to accomplish the needs of either GCM or landscape models. With respect to future development of SVAT models at both scales, there is now a concensus opinion that exchange processes should be related to canopy physiological and ecosystem respiration potentials, thus, preparing an appropriate link to ecosystem dynamics and to biogeochemistry [40]. Similarly, SVAT-model sensitivities with respect to water stress, phenological stages and site-specific nutrient availability is being improved. At both global and landscape scales, the importance of remote sensing for parameterization and ultimately for validation is unquestionable [23, 28, 36, 40]. Differences in global versus regional and landscape scale SVATs may be expected in the structural representation of ecosystems. While it may suffice for GCM applications to differentially define the parallel flux contributions of two or

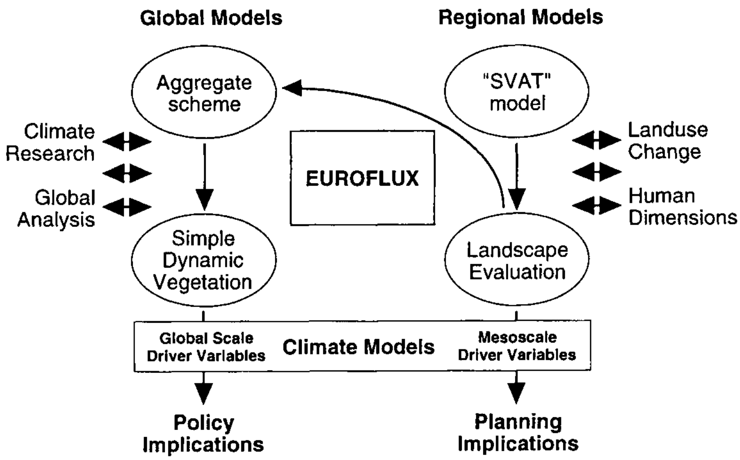

Figure 1. Schematic representation of the dual applications for information gained in the project EUROFLUX (i.e. from coordinated comparative studies of forest gas exchange). Long-term observations of H_2O and CO_2 exchange permit development of a new generation of stand level 'SVAT' models based on ecosystem physiology and biogeochemistry. Since both H_2O and CO_2 exchange are quantified with these models, they provide important interfacing with growth and production models and link via these to landscape assessments, evaluation of land-use change, and, thus, to the international Human Dimensions Programme of IGBP. Such landscape evaluations as well as the flux measurements provide a new and better basis for parameterization of SVAT models designed for large scale applications, i.e. in global models. 'Aggregate SVATs' that include landscape characterization in their parameterization may be related abstractly to vegetation dynamics at large scales. Landscape level SVAT models for specific elements of the vegetation can provide information useful in resource management and planning when coupled with mesoscale climate models. More abstract aggregate SVATs will provide information relevant to broad policy implications when coupled to global scale climate models. The design of a 'realistic' but simplified and efficient SVAT model for landscape applications is one goal being pursued within the EUROFLUX project.

maximally three functional elements per grid square (each with minimum layering), the assignment in development of SVATs at the landscape level is to realistically assess differences in flux regulation by recognizable landscape elements. The simplifications of ecosystem structure and function at both scales should be carried out explicitly.

At landscape scales, the actual performance of individual species should be described. Such models must attempt to reasonably describe average function in 'homogeneous' landscape units with a horizontal dimension of 10 m to 1 km. Current restrictions on the assumption of homogeneity are usually imposed by the resolution of remotely sensed data, e.g. 30 m size of Landsat TM pixels, or by potentials for coupling stand level analyses with other models, e.g. 1×1 km grid size of some mesoscale climate models versus small grid sizes in hydrological models. Whereas global-oriented SVATs must consider large scale disturbance effects on surface exchange, landscape SVATs and landscape ecosystem models will be required to distinguish and alternatively evaluate the effects of differing anthropogenic impacts on integrated landscape function [26]. Thus, mechanistically based model hierarchies must be developed that permit an understanding of function within important ecosystem compartments as well as overall flux rates.

While the EUROFLUX project supports research efforts at several scales, the research papers subsequent in this issue derive from an activity primarily related to landscape and regional perspectives. The workshop entitled 'Water Flux Regulation in Forest Stands' was held in Thurnau, Germany during September 1996 to assess our current understanding of water relations and water balances in European forests. More specifically, recent studies of transpiration via the application of sapflow monitoring methods were highlighted and the new view of water flux regulation that they provide was examined. We hope that the picture presented here will be broadened during the course of EUROFLUX and that a new understanding of the range of behavior possible for European forest stands will result.

2. SIMILARITY AND HETEROGENEITY IN EUROPEAN FOREST ECOSYSTEM FUNCTION

Our understanding of the current forest vegetation of Europe can be related first to the reinvasion of the continent by forest species after the last glaciation [13], but subsequently and more importantly to land clearing and later to broad-scale, intensive forest management practices. While species-specific traits, ecological preferences and competitive potentials provide ecological restrictions on variation in process rates, e.g. potential growth in relation to soil characteristics or atmospheric factors [5, 11], the 'experimental planting' of only a few commercially useful species over large land areas within European countries means that response under sub-optimal conditions often contributes to occurring heterogeneity. Wide-scale plantings have contributed to the world-wide dissemination of knowledge of the physiology and production of such species as *Pinus sylvestris* and *Picea abies* (e.g. Gholz et al. [15]). While certain principles influencing variation in forest ecosystem function have become apparent in examining these data, e.g. dependence of phenological events or changes in rates of biomass accumulation on climate gradients (cf. Bugmann [5]), nutrient availability effects on leaf area index, and the strong correlation of canopy carbon gain with changes in light interception [15], continental scale patterns in the actual exchange of materials between forest vegetation and the atmosphere are much less clear due to interactive effects of nutrient deposition, uncertainty in describing water balance, as yet undefined responses to temperature stress, and incomplete knowledge of the structural changes that occur in trees along with these conditions.

As might be expected, the extensive use of only a few major species has resulted in numerous European studies of forest water balance in stands of pine, spruce, beech and oak. A recent review of European forest literature by Peck and Mayer [25] revealed a reported range in annual transpiration (maximum annual estimate minus minimum estimate) of approximately 600, 400 and 300 mm for *Pinus*, *Picea* and *Fagus,* respectively, and of 720, 690 and 540 mm in mean ET for the same species. Attempts to generalize these results demonstrate that our understanding of shifts in water flux regulation at landscape to continental scales is vague. Large differences in transpirational water use that are reported among stands are not systematically well-explained in terms of 1) experimental difficulties resulting from different methodologies, 2) differences in weather conditions, 3) differences in structure as affected by age and management practices, and 4) differences in stand nutrition, understory flux contributions and interception.

Intensive study but lack of generalizable results provides a contradiction that occurs because of differing methods, experimental design and scales of observation. Sapflow methods that are now becoming increasingly a 'standard tool' in studies of water balance will aid our understanding for forest function by clarifying flux regulation at the individual tree level. Nevertheless, 'standardization' of sapflow measurements must be discussed and attention must be focused on errors and short-comings of the method. We hope that this goal will be promoted by the papers of the proceedings which follow, by new communication networks established at the Thurnau workshop, and through the interaction among research groups of EUROFLUX. Additional contributions from the EUROFLUX project to clarification of continental scale heterogeneity in forest vegetation/atmosphere exchanges and in comparative analysis of flux regulation is anticipated, since a single methodology is used at the stand level for ET and CO_2 exchange measurements. Furthermore, above canopy flux observations are accompanied by a suite of measurements which simultaneously characterize function within individual ecosystem compartments.

3. CONTINENTAL SCALE GRADIENTS, FOREST PLASTICITY AND RESEARCH NEEDS

Climate, variation in species-specific potentials and nitrogen deposition [47] produce a broad range of leaf area indices in the forest stands selected for study by EUROFLUX, differences in light interception and a broad range in annual wood increment *(table I)*. A clear understanding of the multiple influences affecting function in the EUROFLUX stands will be difficult to achieve owing to process interactions, non-linear responses, long-term ecosystem adjustments and difficulties in evaluating the importance of extreme events. Nevertheless, comparative analyses along environmental gradients provide the best clues for explanations (cf. Magill et al. [20]), even though several gradients may overlap in complex fashion and sharp transitions in function should not be expected. A number of the papers included in this issue extend the environmental gradients associated with observations of water fluxes in forest stands, e.g. by including forests of riparian zones and at high elevation mountain sites. The importance of combining information from these sites with information from EUROFLUX locations should not be underestimated. Fundamental information on ecological potentials of plants and regulatory mechanisms has often been gained in habitats that are extreme with respect to particular environmental factors.

Achieving an understanding of forest response and forest acclimation potential along climate gradients and in response to environmental stresses is key to the development of realistic dynamic vegetation models. Available process information determines the structuring of such models, the included parameterization, and, therefore, their overall behavior, e.g. whether transitions along continental level transects are correctly described and whether important vegetation/atmosphere feedbacks are quantified. Forest biologists must examine and improve the assumptions of such models via coordinated comparative process studies. With respect to European forests, response 'strategies' of spruce, pine, beech and oak, as well as those species occupying extreme situations or special habitats must be defined. The question of how phenology, structural change and physiological plasticity change

Table I. Characteristics of the forest stands currently being studied by the project EUROFLUX arranged from south to north.

Site	Position	Elevation (m a.s.l.)	Overstory species	Understory species	Mean T (°C)	Precipi-tation (mm)	LAI (m^2 m^{-2})	Canopy height (m)	Stand age (years)	Density (n ha^{-1})	Wood increment (m^3 ha^{-1} $year^{-1}$)
Italy	41°45'N 12°22'E	3	*Quercus ilex*	evergreen shrubs	15.3	770	3.5	12.5	50	1500	3.5
Italy	41°52'N 13°38'E	1550	*Fagus sylvatica*	herbs, cf. *Gallium*	7	1 100	4.5	22	100	890	7
France	44°42'N 0°46'W	60	*Pinus pinaster*	*Molinia caerulea*	13.5	900	3	18	35	500	18
France	48°40'N 7°05'E	300	*Fagus sylvatica*	*Carpinus betulus*	9.2	820	5.5	13	30	4 000	no data
Germany	50°09'N 11°52'E	780	*Picea abies*	*Deschampia flexuosa*	5.8	890	6.5	19	45	1 000	5
Belgium	50°18'N 6°00'E	450	*Picea abies*	mosses	7	1 000	4.5	27	60–90	200	7
Germany	50°58'N 13°38'E	380	*Picea abies*	*Deschampia flexuosa*	7.5	820	5	28	105	650	11
Belgium	51°18'N 4°31'E	10	*Pinus sylvestris*	herbs	10	750	3	22	70	540	7
Netherlands	52°10'N 5°44'E	25	*Pinus sylvestris*	*Deschampia flexuosa*	12	800	3	15	100	360	6.3
Denmark	55°29'N 11°38'E	40	*Fagus sylvatica*	herbs, cf. *Anemone*	8	600	5	25	80	430	no data
UK	56°37'N 3°48'E	340	*Picea sitchensis*	mosses	8	1 400	8	6	15	2 500	14
Sweden	60°05'N 17°28'E	45	*Pinus sylvestris* *Picea abies*	*Vaccinium*, mosses	5.5	530	5	25	100	600	5
Finland	61°51'N 24°17'E	170	*Pinus sylvestris*	*Vaccinium spp.*	3.5	640	3	12	30	2 500	10
Iceland	63°50'N 20°13'W	78	*Populus trichocarpa*	grass and mosses	3.6	1 120	2.5	1	7	10 000	no data
Sweden	64°07'N 19°27'E	225	*Picea abies*	———	1	570	2	8	30	2 100	2.6

along gradients in resource availability and, thus, control fluxes, biogeochemical cycles and competitiveness must be systematically addressed.

It is particularly important to obtain a broader understanding of the effects of water stress on forest gas exchange. Decreased water availability significantly influences ecosystem function of all major European forest types, from boreal forests of Scandinavia to Mediterranean forests and shrublands [8, 34, 35, 43, 44, 46]. From north to south in Europe, there are obviously large differences in the duration and frequency of drought, its predictability, and the depth to which soil dries. While current summaries of information on forest gas exchange response have generally defined the relationship between soil water availability and forest canopy conductance [18], there are few systematic studies of variability in this response with respect to soil type or along climate gradients at landscape or continental scales (as, for example, with respect to location on slopes for *Quercus ilex*; Sala and Tenhunen [34]). Interpretation of shifts in the response to water stress for selected forest stands along topographic gradients, e.g. changes in physiology versus structure, will provide the basis for adjusting flux estimates applicable at large scales. It should be noted that most descriptions of forest gas exchange response to water stress do not consider the behavior of the understory and provide no information on potential changes in flux partitioning that may occur. Since forest understory species appear differentially adapted to water stress and exhibit differing strategies of water use [48], additional studies are required to clarify changes in flux partitioning and changes in total ecosystem gas exchange during the course of soil drying as well as after rehydration.

Current knowledge of major processes affecting forest ecosystem function along precipitation and temperature gradients in the Alps has been summarized in the model FORCLIM [5]. This summary serves as an interesting precursor model for attempts to relate site conditions (monthly mean temperatures, monthly precipitation, nitrogen availability, winter cold temperatures and summer drought) to forest community composition and biomass accumulation at European continental scales. The results of the simulation studies suggest that prediction of changing species dominance and of biomass accumulation within the selected climate space is possible. Nevertheless, major problems occur in predicting forest response with limited water availability. Furthermore, only crude estimates of forest/atmosphere exchanges (carbon gain, pollutant uptake, emission of VOCs, etc.) and no quantification of flux partitioning among species is currently possible at regional to continental scale.

A much closer cooperation is needed, as proposed within the EUROFLUX project, between research groups developing dynamic vegetation models and those quantifying forest ecosystem atmospheric exchanges and water balance. The shortcomings of dynamic vegetation models may be related in part to our current inability to adequately generalize water availability effects due to rainfall patterning as well as exposition or landscape position effects on forest ecosystem structure and function [3, 22, 34]. This collection of papers resulting from the workshop 'Water Flux Regulation in Forest Stands' represents a step in the effort to assess current knowledge of forest water balances, to determine how to generalize this knowledge, to include it into simulation models, and to subsequently document our current understanding with model tests. Thus, this issue represents work dedicated to building new measurement and communication networks, to developing ideas for upscaling, and for integrating information on fluxes and biogeochemistry at landscape, regional, and continental scales.

ACKNOWLEDGEMENTS

We are grateful for support of the workshop 'Water Flux Regulation in Forest Stands' provided by the Bundesministerium für Bildung, Wissenschaft, Forschung und Technologie, Germany (BEO 51-0339476A) to BITÖK, by the EC EUROFLUX project (ENV4-CT95-0078), and by the international BAHC core project office in Potsdam, Germany.

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