

WORKSHOP PROCEEDINGS 2001-11

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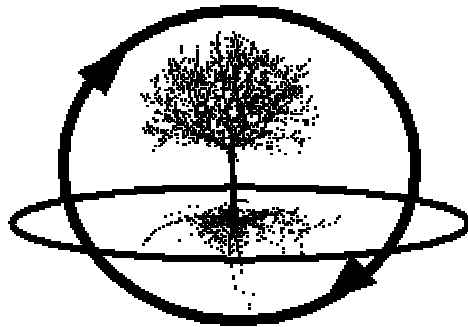
**Third International Workshop
on Functional-Structural
Tree and Stand Models**
September 27 - 30, 2001
Val-Morin, QC

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**Third International Workshop
on Functional-Structural Tree and Stand Models**



Val-Morin (Québec), Canada

September 27-30, 2001

PROGRAM

Thursday, September 27th: from 19:00 to 23:00

Registration and welcoming cocktail

Friday, September 28th

8:30 Welcoming speech by the organisers of the conference

Session A. Representation of tree architecture, stand structure, tree and stand environment and resource capture: aboveground and belowground.

8:50 **Frédéric Boudon**, Christophe Nouguier and Christophe Godin
Title: Multiscale geometric representation of heterogeneous stands.

9:15 **Jean Dauzat**, D. Luquet and A. Begue
Title: Energy balance modelling and thermography simulation on 3D plant models.
Application on cotton trees.

9:40 **Sylvain Delagrangé**, Eero Nikinmaa, Pierre Dizengremel, and Christian Messier
Title: Strategies of biomass allocation in understory hardwood trees.

10:05 **Przemyslaw Prusinkiewicz**
Title: L-systems as the platform for functional-structural plant modeling.

10:30 break

11:00 **Pascal Ferraro**, Lars Muendermann, Przemyslaw Prusinkiewicz and Christophe Godin
Title: L-systems and MTGs: Integrating simulation and formal analysis of architectural plant models.

11:25 **Pekka Nygren**, Harry Ozier-Lafontaine and Risto Sievänen
Title: Modelling the sharing of soil resources in agroforestry systems.

11:50 **Jari Perttunen**, Eero Nikinmaa and Risto Sievänen
Title: Enhancing the capabilities of the functional-structural tree model LIGNUM with Lindenmayer-systems and generic programming.

12:15 Lunch

13:30 Formal Poster session with researchers

15:25 **Kenneth J. Stadt** and Victor J. Lieffers
Title: Modelling light transmission at the stand and microsite level in the boreal forests of Alberta and Quebec.

15:50 **Przemyslaw Prusinkiewicz** and Brendan Lane
Title: Integrating L-system models of plant architecture and plant ecosystems.

**Session B. Resource use and internal processes : hydraulic architecture,
carbon and nitrogen transport and allocation, phenology.**

16:15 **Pekka Kaitaniemi**
Title: Canonical modeling and allometric scaling of canopy structure: simplifying representation of internal processes in mountain birch.

16:40 **Theodore DeJong**, Przemyslaw Prusinkiewicz and Mitch T. Allen
Title: Using L-systems to model carbon transport and partitioning in developing peach trees.

17:05 Synthesis I by invited speaker + discussion

19:00 Supper

21:00 Live music (mainly jazz)

Saturday, September 29th

8:30 **Anna Sala**
Title: Hydraulic sufficiency of conifers depends on size-dependent changes of leaf to sapwood ratios.

8:55 **Jian Wang**
Title: Comparison of spring and summer hydraulic properties of 14 tree species of boreal forest in British Columbia.

9:20 **Kihachiro Kikuzawa**
Title: Changes in Light Interception and Photosynthetic Rate with Time in Relation to Leaf Emergence Patterns.

**Session C. Presentation of various tree-level and
stand-level functional-structural models**

9:55 **Helge Dzierzon** and Winfried Kurth
Title: Simulation of tree stands using L-Systems and the assessment of results shown by a Scots pine stand example.

10:20 Break

10:45 **Rüdiger Grote**
Title: A model for simulation of long-term competition effects in mixed forests

11:10 **Takashi Kohyama** and Takuya Kubo
Title: Population-level processes of overcrowded subalpine fir stands, reconstructed from a shoot-based simulator of tree architecture.

12:00 Lunch

13:15 Walk in the bush

- 15:15 **Risto Sievänen**, Pekka Nygren, Frank Berninger and Eero Nikinmaa
Title: Coupling a transport/resistance model of allocation with a model of crown architecture.

Session D. Concrete examples of utilization of functional-structural tree and stand models in forestry and agro-forestry.

- 15:40 **Veli-Pekka Ikonen**, Heli Peltola and Seppo Kellomäki
Title: Modelling the structural growth, stem and wood properties of Scots pine (*Pinus sylvestris* L.) related to silvicultural management with implications in simulated sawing.
- 16:05 **Danielle J. Marceau**
Title: Complex systems theory and forest dynamics: What can we learn from the SORTIE model?
- 16:30 **André Ménard**, Danielle J. Marceau, André Bouchard, Patrick Dubé and Charles D. Canham
Title: Tree release episodes in the neighborhood of small-scale disturbances (SSD): a modelling assessment of SSD extent and impact.

16:55 Synthesis by invited speaker + discussion

17:40 Models demonstration

19:00 Supper with live classical music!

Sunday morning, September 30th

8:30 to 10:00 business meeting (future meeting, collaboration and exchange of data and info among Tree and Stand structural and functional models)

11:30 to 16:00 trip to St-Sauveur for Shopping and sightseeing

16:00 return to Dorval Airport (at around 17:00)

Poster Session

Marilou Beaudet, Christian Messier and Charles D. Canham

Title: Effect of different partial harvesting scenarios on understory light conditions in northern hardwood stands: simulation with the SORTIE light model.

Olevi Kull, Ingmar Tulva and Elina Vapaavuori

Title: Consequences of elevated CO₂ and O₃ on birch canopy structure: implementation of the canopy growth model.

Kiyoshi Umeki

Title: Effect of light intensity on the allocation of growth in young *Betula platyphylla* saplings.

Danilo Dragoni, A.N. Lakso and S.J. Riha

Title: Approaches to modeling water fluxes through soil-plant-atmosphere continuum in an apple orchard.

Yann Nouvellon, Saint-André, L., Dauzat, J., Roupsard, O., Caraglio, Y., Hamel, O., Berbigier, P., Bonnefond, J-M., Irvine, M., Mabilia, A., Epron, D., Mouvondy, W., Laclau, J-P., Bouillet, J-P., Jourdan, C.

Title: Linking tree architecture and function for continuous simulations of carbon, water and energy fluxes from Eucalyptus stands in Congo.

Rüdiger Grote

Title: A model for simulation of long-term competition effects in mixed forests.

Kenji Seiwa, Takahiro Kadowaki, Sigetoshi Akasaka, and Kihachiro Kikuzawa, Kadowaki

Title: Shoot life-span in relation to successional status for 15 deciduous broad-leaved tree species.

Naoto Ueno and Kenji Seiwa

Title: Intersexual differences in shoot architecture and functions in a dioecious tree, *Salix sachalinensis*.

Frédéric Raulier, Pierre-Yves Bernier, Chhun-Huor Ung, Richard Fournier, Luc Guindon and Jacques Régnière

Title: Error estimation on net primary productivity predictions at the landscape level in the boreal forest of Eastern Canada.

André Lacoite

Title: Rendering the effect of source-sink distances in whole plant carbon partitioning models.

Christiane Eschenbach

Title: Validation of the photosynthesis module of ALMIS at leaf, shoot and whole tree level.

Daniel Mailly, Sylvain Turbis, Stéphane Poirier and Richard Fournier

Title: Influence of crown shape and distribution on light interception: application of a light model and implications for stand-level modelling.

Sylvain Turbis and Daniel Mailly

Title: OpenGL and PovRay as powerful tools to visualize and analyse stand structure in a forest simulation model.

Karin Rebel and S. J. Riha

Title: A Spatial Explicit Model of Water Uptake by Trees in a Watershed.

Erwin Dreyer, Pierre Montpied, Sylvain Delagrangé, Piotr Robakowski, Delphine Retzinger, Pierre Dizengremel, François Alain Daudet, Xavier Leroux

Title: Parametrisation of leaf photosynthesis models in seedlings from a range of broadleaved tree species grown under diverse irradiance microclimates.

Manfred Küppers, Ralf List, **Christiane Eschenbach**

Title: MADEIRA: Simulating Environmentally Sensitive Growth of Canopy Architecture as Based on Woody Plant Physiology and Morphology - Examples and Applications

Belinda Medlyn, Paul Berbigier, Achim Grelle, Denis Loustau, Sune Linder

Title: Two Contrasting Flux Sites Used To Test A Model Of Forest Canopy Gas Exchange

Pepper, D.A., **McMurtrie, R.E.**, Medlyn, B.M., Owensby, C.E. and Linder, S.

Title: Carbon sink responses of grassland and forest ecosystems to increasing atmospheric CO₂ concentration, rising temperature and increasing nitrogen fixation

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Presentation abstracts

Frédéric Boudon, Christophe Nouguier and Christophe Godin

Multiscale geometric representation of heterogeneous stands.

The aim of this talk is to present a general geometric model for plant representation that considers different plant perceptions at different levels of organization (or scales).

Abstract

This model is based on a representation of plant topology that integrates several scales within a single framework. This model, called Multiscale Tree Graph (MTG), can be seen as a set of recursively nested graph, representing different levels of topological organisation. Each entity of a MTG, at any scale, can be augmented with a geometric model. Several geometric representations of the plant can thus be computed, depending on the scale considered to represent geometry. Since these models are geometric representations of the same real object at different scales, they must be consistent with one another. To ensure model definition consistency, within-scale and between-scale constraints are introduced. This constraints enable flexible management of "multiscale geometric models".

Multiscale geometric models can be used to compute geometric representations of plant architecture that are best adapted to some particular criteria. For example, in tree simulation, computer applications are often limited by the tremendous amount of topological and geometric data resulting from the simulation engine. Multiscale geometric models can be used to control the amount of memory used by the representations. It allows us to obtain, for example, compressed plants representations. Different possible applications of this multiscale geometric model to the representation of stands are finally discussed.

J. Dautzat, D. Luquet and A. Begue

**Energy balance modelling and thermography simulation on 3D plant models.
Application on cotton trees**

Infrared thermography interpretation for monitoring water status of sparse and/or heterogeneous canopies faces the problem of the determination of sunlit and shaded fractions of soil and vegetation within the camera field. In order to analyse canopy thermographies, an integrated model has been developed using 3D plant models. The working level of the model is the plant organ for vegetation and square patches for soil. For each time step, iterative calculations of plant organ irradiation, stomatal conductance and energy budget are performed leading to a first estimation of organ temperature. In parallel, the temperature of soil patches is calculated using a model adapted from Noilhan and Planton which integrates both the temperature and the water balance for 2 soil layers. Sensible and latent heat fluxes emanating from soil and vegetation are then used to simulate the air temperature and humidity profiles within the canopy. According to the new profiles, the energy budget of canopy elements is reactualised. When transient equilibrium is reached, the temperature of plant organs and soil patches is saved in a file which is used later on for thermal infrared visualisation of the scene.

Simulated cotton tree thermographies are compared to field thermographies for different water regimes and growth stages for validation. The effect of plant architecture on the thermal infrared signal is then analysed through sensitivity analysis vs. branch geometry and leaf inclination angles. Finally, the capability of infrared thermography to assess water stresses is discussed for varying sun-sensor geometry conditioning the sunlit and shaded fractions of soil and vegetation within the camera field.

Sylvain Delagrangé, Eero Nikinmaa, Pierre Dizengremel, and Christian Messier

FSM-modelling facilitates interpreting the performance of tree seedlings in gap environment in terms of physiological and morphological traits

The replacement of mature trees temporarily modify environmental conditions. Such perturbations form gaps that create a wide range of light levels in the understory. Long-term observations made in Michigan (USA), indicated detrimental effects on yellow birch regeneration as gap size decrease. On the contrary, sugar maple seemed to be well adapted to regeneration in small as well as large canopy gaps.

In order to understand these trends better, we examined carbon assimilation, carbon allocation and architecture of yellow birch and sugar maple seedlings and saplings in field conditions. The measurements were made on seedlings and saplings of different heights (20cm to 500cm) grown under a gradient of light availability (0.5% to 35%). The impact of morphological and physiological traits on whole plant carbon balance was evaluated in the two co-occurring species.

Results show that increasing tree height changes the tissue mass ratio to unfavourable direction (i.e. increases of unproductive tissues dry mass %). However, increases in height provide higher root prospecting, available lights and greater leaf areas that, in turn, increase light capture and seedling photosynthetic capacities. Clear differences between species are difficult to establish. Indeed, tree understory survival or tree shade tolerance seems to be defined by the sum of numerous morphological and physiological traits that may differ from a tree to another.

Functional-structural modelling offers a possibility to link these traits together to evaluate seedlings and saplings behaviour in variable environment. Such models permit the evaluation of the relative importance of different traits on seedling performance. Here we use our measurement of assimilation, architecture and allocation to parameterize a functional-structural model of tree growth (LIGNUM, Pertunen *et al*, 1996; 1998) on both species. We subsequently use the model to study the relative importance of architectural and physiological traits on tree growth. Finally we compare the simulation results with the fields observations to evaluate significance of the results.

Przemyslaw Prusinkiewicz

L-systems as the platform for functional-structural plant modeling

L-systems were originally introduced to model the development of relatively simple multicellular organisms, such as algae [Lindenmayer, 1968], yet they are currently widely used in the modeling of higher plants, including functional-structural modeling [Mech and Prusinkiewicz, 1996, Prusinkiewicz *et al.*, 1997]. Are L-systems merely one of many alternatives, or are they *the* formalism for functional-structural modeling, the point of convergence of the multiple approaches that have been proposed so far? In my presentation I will attempt to support the second point of view, by showing that L-systems capture the essential processes of development identified by Coen [1999], as long as they are confined to branching structures considered at the modular level. On this basis, I will address the following questions:

- What is the correspondence between components of functional-structural models and constructs of L-system-based programming languages?
- What might be the theoretical or practical reasons for *not* using L-system-based approaches and software in specific functional-structural simulations?
- What might be the theoretical or practical reasons for combining L-system-based simulations with the use of external programs that simulate specific physiological processes?

The presentation is intended to stimulate a discussion on the prospective directions of the L-system-based functional-structural modeling methodology.

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Pascal Ferraro, Lars Muendermann, Przemyslaw Prusinkiewicz and Christophe Godin

L-systems and MTGs: Integrating simulation and formal analysis of architectural plant models.

The formalism of multiscale tree graphs (MTGs) was introduced in 1998 by Godin and Caraglio [3] to represent plant topology at different scales and levels of abstraction, for instance the levels of metamers, growth units, and plant axes. Once represented in the form of an MTG, plant data can be explored using software AMAPmod [4]. Tools included in AMAPmod make it possible to discover regularities in plant structures, quantify differences between given branching structures, and perform many other analytical tasks [2,5].

MTGs may represent experimental data, obtained by measuring plants, and plant structures modeled using simulation programs. Our presentation will focus on plant models specified using L-systems [7]. We will discuss an algorithm for converting plant structures generated with L-systems into the MTG format and an implementation of this algorithm in the modeling program cpfg [6]. The virtual laboratory software (vlab) [1] is used to integrate cpfg, developed at the University of Calgary, and AMAPmod, developed at Cirad, into a cohesive system for modeling and analyzing plants. We will present sample applications of this system, and focus on an example of its application to the analysis of self-similarity in measured and modeled inflorescences of *Syringa* species.

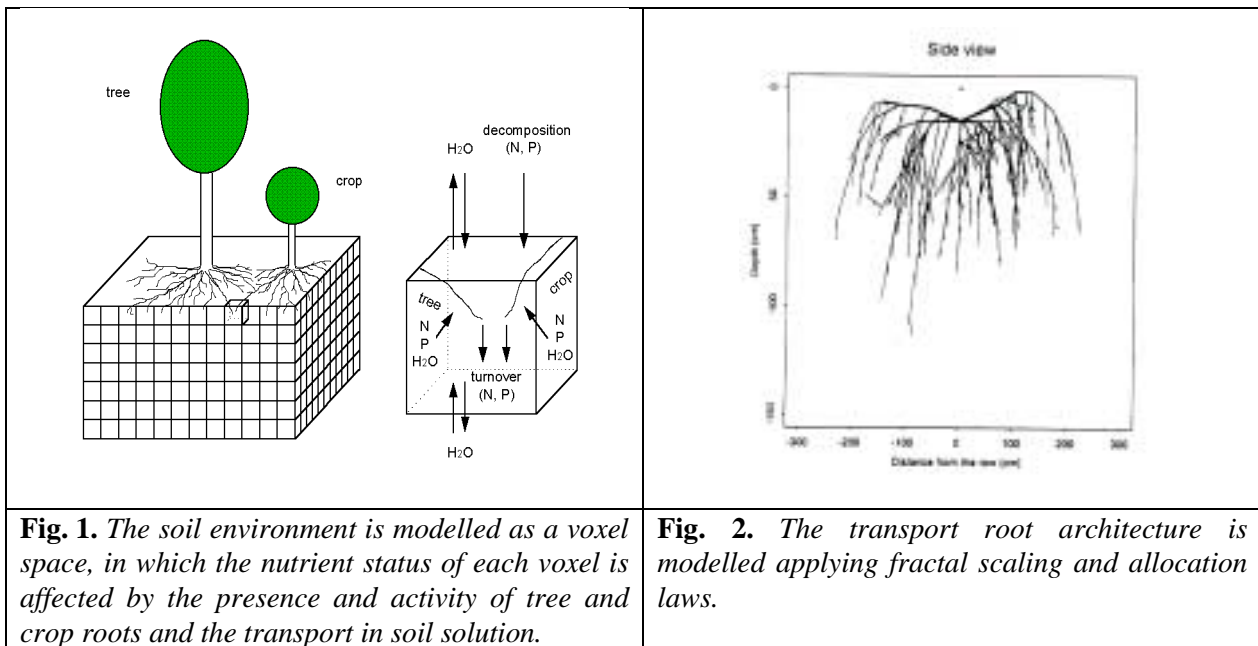
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Modelling the sharing of soil resources in agroforestry systems.

Agroforestry systems (AFS) are agroecosystems composing of trees and crops sharing the same field. Understanding the sharing of soil nutrients is a key issue for successful development of these cropping systems. The 3D structure of root systems has an important effect on the sharing of soil resources, because the roots extract nutrients from the soil environment characterised by an important spatial variation and the root architecture defines the sharing of soil space. The nutrient extraction by plants modifies the soil environment. Our aim is to model the regulation of root growth and sharing of soil N and P resources as affected by root functions and architecture in AFS.

A module describing N and P uptake and N₂ fixation within the 3D architecture of the root system will be developed for the functional-structural tree model LIGNUM (www.metla.fi/projects/lignum). Within the voxel space (Fig. 1), the woody transport roots are considered as the skeleton of the root system (Fig. 2), in which the functionally active fine roots and N₂-fixing nodules are attached. The growth and turnover of fine roots is regulated by N and P availability. The uptake of N and P, as well as N₂ fixation in the legume species, is affected by nutrient availability in soil and demand in canopy.



The modelling work is in a preliminary phase. So far, we have applied the fractal root architecture model to the tropical legume trees *Gliricidia sepium* (Jacq.) Kunth ex Walp and *Erythrina lanceolata* Standley. The scaling and allocation factors are independent on root diameter and the same parameter values apply over the whole root system. When metabolic differences of principal N sources (NO₃⁻, NH₄⁺ and N₂ fixation) are taken into account, the modelling approach realistically simulates the regulation between N₂ fixation and uptake of mineral N.

Jari Perttunen, Eero Nikinmaa and Risto Sievänen

Enhancing the capabilities of the functional-structural tree model LIGNUM with Lindenmayer-systems and generic programming.

The functional-structural tree model LIGNUM presents a tree with four structural units called bud, branching point, tree segment and axis that have close counter parts in real trees. LIGNUM has been successfully applied to both coniferous and hardwood tree species, see for example [1] and [2].

LIGNUM has been implemented with a general purpose programming language C++. The rules of architectural development for the tree species modeled with LIGNUM have consequently been *ad hoc* descriptions of the branching. This is inferior to using a formal way, such as Lindenmayer-systems, for describing architectural development. In order to improve the capabilities of LIGNUM, we have implemented part of the language L defined by [3] in it. This allows the modeler to define the structural development of a tree with Lindenmayer systems in LIGNUM; we present examples of such simulations.

Secondly, we describe how the object-oriented program design of LIGNUM has been changed to so-called generic programming design. It allows us to define a tree as an abstract datatype that improves the possibilities of model reuse. Finally, we discuss some computational complexity issues regarding modeling the metabolic processes and flow of information in a tree and propose four simple linear time generic algorithms as a generic computational framework.

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Kenneth J. Stadt and Victor J. Lieffers

Modeling light transmission at the stand and microsite level in the boreal forests of Alberta and Quebec.

We developed, MIXLIGHT, a light transmission model for boreal mixed-species forest stands which functions at two scales: stands and microsites. Both scales use a ray-tracing algorithm to sample the canopy, and attenuate light along each ray according to standard light penetration theory. The stand-level model operates on the assumption of random leaf area distribution across the entire stand while the microsite model allows for foliage grouping into single-tree crowns. The model is designed to work with the minimal data contained in an inventory plot plus leaf area density and leaf inclination parameters typical for boreal forest species. Model predictions were tested in independent plots using field light measurements. The cost and advantages of the microsite vs. the stand-scale model are evaluated with respect to forest understory development.

Integrating L-system models of plant architecture and plant ecosystems

The need for biologically plausible and visually realistic simulations of plant ecosystems occurs in many applications, including computer-assisted landscape and garden design, visual impact analysis of forest regrowth after logging, and the visualization of ecosystem dynamics for research and educational purposes. We manage the complexity of these simulations using the hierarchical (two-level) modeling approach proposed by Deussen *et al.* [1998]. It consists of the following steps:

1. Individual-based simulation of a plant ecosystem, using coarse representations of individual plants. This step establishes positions and general characteristics of the plants, such as their height, diameter, and the overall shape of tree crowns.
2. Generation of detailed plant models that satisfy the characteristics determined in the previous step.
3. Realistic visualization of the ecosystem, using detailed plant models substituted for their coarse counterparts.

We show that L-systems can conveniently be used in steps 1 and 2 of the modeling process. Step 1 is based on the notion of *fragmentation*, which makes it possible to capture sexual reproduction and asexual propagation of plants [Rozenberg *et al.*, 1976]. We introduce *multiset L-systems* as a generalization of L-systems with fragmentation, and extend previous definitions of the geometric (turtle) interpretation of L-systems and the communication of L-system models with the environment [Mech and Prusinkiewicz, 1996] to multiset L-systems. The resulting formalism provides a tool for specifying individual-based ecosystem models and simulating their development over time. Once an ecosystem has been simulated, we use the global-to-local methodology for plant model construction [Prusinkiewicz *et al.*, 2001] to convert coarse plant representations in the individual-based model into more detailed representations suitable for visualization purposes. Sample applications of the resulting method include self-thinning in a monoculture of plants, emergence of clustering in plant distribution, and succession of trees in a forest.

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Pekka Kaitaniemi

Canonical modeling and allometric scaling of canopy structure: simplifying representation of allocation processes in mountain birch

Allometric scaling laws predict several design principles for the 3D structure and functioning of trees. Therefore, models based on simple scaling laws may potentially serve as an alternative for more detailed physiological models of allocation processes. I investigated the importance of allometric scaling laws for growth and 3D structure of mountain birch. The stem volume of 45 trees was estimated by digitizing tree architecture and using additional measurements of stem and branch diameter. The measurements were transformed into biomass by using stem density estimates from neighbouring trees of equal size. Allometric scaling exponents were calculated for the relationship between tree mass and structural variables such as leaf number, leaf area, stem diameter and tree height. In general, the confidence limits of the exponents detected in mountain birch were found to encompass theoretical values (Fig. 1). Similar scaling exponents were detected at different hierarchical levels of architecture.

In addition, I investigated the importance of the principle that resource transport is most efficient when the distance between a source and a sink is smallest, i.e. when a tree canopy has a compact form. This was done by examining the relationship between long shoot length and its distance from the base of the stem. Transport distance set a clear maximum for long shoot growth (Fig. 2), possibly indicating limits to the amount of resources that can be transported to a distant sink. A lot of unexplained variation remained below this maximum (Fig. 2). Therefore, additional factors have to be considered in a mountain birch model to account for this variation. Canonical modeling, power-law estimation of resource fluxes, may be used as a simple method to integrate the effects of allometric design principles and the modifying additional variables without the need to invoke direct modeling of physiological processes in a model of mountain birch architecture.

Conclusions:

- allometric scaling largely determines resource allocation within mountain birch canopy
- growth is constrained by transport distance from a source
- canonical modeling enables easy integration of allometric scaling and environmental variables in an architectural tree model

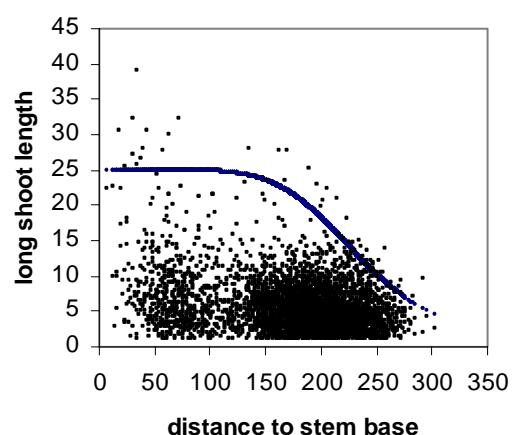
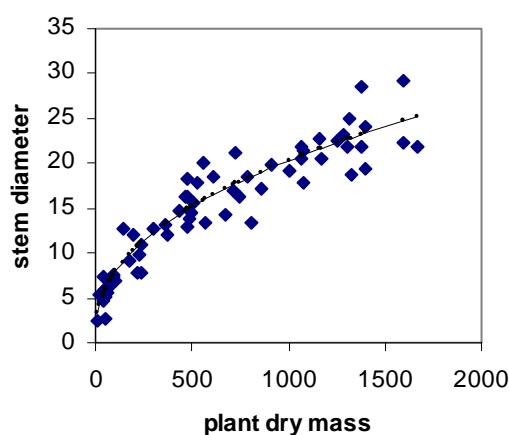


Fig. 1. An example of allometric scaling of mountain birch structure. The theoretical scaling exponent 0.375 is within the estimated confidence limits 0.37-0.46.

Fig. 2. The relationship between transport distance and long shoot growth.

Theodore DeJong, Przemyslaw Prusinkiewicz and Mitch T. Allen

Using L-systems to model carbon transport and partitioning in developing peach trees.

Previously, Grossman and DeJong developed the model “PEACH” to simulate the growth of peach trees based on the hypothesis that carbon partitioning within the tree is driven by competition among sinks. In these simulations, sinks were generalized compartments that included maintenance respiration, leaves, fruits, stems, branches, trunk, and roots. More recently, we have begun to use L-systems to extend these modeling efforts to explicitly include canopy architecture in the simulation of carbon partitioning and growth. This approach, in which various components of the canopy interact as semi-autonomous elements of a complex network, has provided a context for exploring the influence of canopy architecture on source-sink interactions within a growing tree canopy. Each internode of the shoot system is represented as a finite element of a resistor network, which functions to connect carbon sources and sinks into a simulated tree canopy. Carbon is loaded at the sources (typically leaves) in such a way as to maintain a locally constant sugar concentration for the duration of one time step of the model, which represents one day of growth. The magnitude of a given leaf’s “potential” is a function of its simulated daily exposure to light combined with its photosynthetic properties. At each sink, the sink potential is a function of the influx of carbon from the previous time step combined with the rate of unloading from that sink. Carbon unloading at sinks is assumed to occur as a Michaelis-Menten like function, with specific values of V_{\max} and K_m at each sink determined by characteristics such as: sink type, age, and size. Carbon flow from sources to sinks is determined for each time step using the current values for each source and sink potential, combined with the resistances of each internode and the overall topology of the canopy. At the end of each computational cycle, the potential at each sink is updated, and growth of the sink is calculated as a function of its carbohydrate accumulation for that time step. In this manner, carbon is partitioned and canopy growth occurs as a byproduct of the interaction between a large number of individual sources and sinks, rather than as the result of a whole-tree level set of allocation and growth rules.

Anna Sala

Hydraulic sufficiency of conifers depends on size-dependent changes of leaf to sapwood ratios.

Evidence suggests that as trees grow older and larger, their hydraulic conductance decreases causing stomatal closure and low photosynthesis rates. This "hydraulic limitation hypothesis" has been proposed as one of the mechanisms responsible for the decline of productivity of old trees and forests. If large trees experience greater stomatal closure than smaller trees, then leaf area-based whole-tree water use should decline with tree size. We tested this hypothesis for three pairs of Rocky Mountain conifers. In the subalpine zone, we sampled whitebark pine (*Pinus albicaulis*) and subalpine fir (*Abies lasiocarpa*). At lower elevations we sampled Douglas-fir (*Pseudotsuga menziesii*) and western larch (*Larix occidentalis*) in a mixed stand and Douglas-fir and ponderosa pine (*Pinus ponderosa*) in another stand. We measured whole tree water use with sapflow techniques in 9-20 trees of different sizes for each species and stand under high water availability. We then determined size-dependent changes in leaf to sapwood area ratios ($A_L:A_S$) by harvesting all trees measured (whitebark pine-subalpine fir and Douglas-fir-western larch pairs) or by using pre-existing local biomass allocation regressions (ponderosa pine-Douglas-fir pair). Integrated daily sapflow on a leaf area basis declined significantly with tree size for whitebark pine ($r^2=0.46$, $p = 0.03$) and western larch ($r^2=0.45$, $p=0.02$) but not for subalpine fir, Douglas-fir and ponderosa pine. Constant or increasing leaf area based sap flow with tree size for subalpine fir, Douglas-fir and ponderosa pine were related to either constant or significant decreases of $A_L:A_S$ ratios with tree size. Decreased leaf area-based sap flow for large whitebark pines and larches were related to significant increases of $A_L:A_S$ ratios with tree size. We conclude that not all trees become hydraulically limited as they increase in size and that size-dependent changes of $A_L:A_S$ ratios have a strong influence on the supply of water to foliage as trees grow large.

Jian Wang

Comparison of spring and summer hydraulic properties of 14 tree species of boreal forest in British Columbia.

Little is known with respect to the seasonal change of hydraulic conductivity of major tree species in the boreal forests. The objectives of the study were to determine and compare the spring and summer Huber value, specific hydraulic conductivity and leaf-specific hydraulic conductivity of 14 tree species of boreal forests. The 14 tree species were divided into angiosperms and gymnosperms. The hydraulic conductivity was measured by gravimetric measure of water flux in excised shoot segments. All gymnosperm species had significantly higher Huber values than angiosperm species except for larch which is a deciduous species. In contrast, angiosperm species had significantly higher leaf-specific hydraulic conductivity in summer. The specific hydraulic conductivity is significantly lower in summer after leaf-out than in the early spring before leaf-out. Deciduous species, on average, showed greater vulnerability to freezing-induced embolism during winter than evergreen conifers species. The results have important implications on the effects of climatic change on plant water use efficiency.

Kihachiro Kikuzawa

Changes in Light Interception and Photosynthetic Rate with Time in Relation to Leaf Emergence Patterns.

Two types of leaf emergence patterns have been observed in trees. One is simultaneous type (flush type) where many leaves appear simultaneously within a single, short period. Shoots of this type also elongate within the short period. The other is successive (succeeding) type where leaves appear one by one successively within a longer period. I investigated the relationships between leaf emergence patterns and light interception and photosynthetic rate of each leaf within a shoot of herbaceous and woody plant species of the two contrasting leaf-emergence patterns. Leaves appeared simultaneously in the two species of flush type, *Polygonatum* and *Fagus*, within a short period in April and May. While leaves appeared one by one successively in the two species of successive type, *Polygonum* and *Alnus*, from May to August (October). Average of total number of leaves emerged on a shoot was far more in the two species of successive leaf-emergence than the two species of simultaneous leaf-emergence. However, number of leaves actually attaching the shoot is not substantially different between each two species pair. In the two herbaceous species, *Polygonatum* and *Polygonum*, about 10 leaves per shoot were attached to a shoot on average from May (June) to August. In the two woody plant species, *Fagus* and *Alnus*, about 5 leaves on average were retained on a shoot from May (June) to September (October). Ages of leaves in the flush species are restricted within two classes of ten-day interval in each of the study periods. These age classes shifted towards higher ages with the progress of time. Leaf-age structures of the successive species were essentially constant within the season. In any time of the season, youngest age-class was observed. The photosynthetic production of simultaneous-type leaf population decreases with progress of time. However, the photosynthetic gain by leaf populations of successive type species does not decrease with time but remains usually high. The stable photosynthesis of leaf-population in the latter type is maintained by the turn-over of leaves throughout a season.

Helge Dzierzon and Winfried Kurth

Simulation of tree stands using L-Systems and the assessment of results shown by a Scots pine stand example

A collection of trees growing in a defined area is called 'tree-stand' or just 'stand'. We show an example of a functional-structural stand model which is implemented using sensitive L-Systems as the software GROGRA processes them. The example contains a model of a simple and homogenous Scots pine (*Pinus sylvestris* L.) stand. Simple presumptions are made to simulate the shape of individuals and interactions between them. The shape of individuals is represented by a single stem and a simplified crown. The crown shape is modelled as a pyramid with irregular bases. The irregular basal area is fixed in eight directions according to cardinal-points. The interaction is based on the distances to next neighbours and their effects on crown radius increments.

Another focus lies on the general assessment of quality regarding results of stand simulations. It seems that stand simulations get more and more practical impact. The parameters which are needed in practice are usually not simulated directly. They have to be obtained from the simulation results by further calculations. That opens the necessity to assess the quality of simulation results concerning such aggregated parameters. We show possibilities to give answers to such problems.

Conclusions:

Using L-systems is a very useful method to implement stand models. They are transparent and easy to publish. Hence they are easy to reproduce by others.

Especially sensitive L-systems as GROGRA processes them allow to simulate interactions between individuals with their neighbours or even some interactions with their environment in general.

Parameters derived from simulation results may respond to stochastic components included in stand models. That underlines the importance to validate models if one wants to use the simulation results in practice.

Rüdiger Grote

A model for simulation of long-term competition effects in mixed forests

A new tree growth model (BALANCE), which considers crown expansion from the outcome of physiological processes, is presented. The processes are driven by individual environmental conditions, including climate, deposition, and air chemistry, which are estimated from field conditions and stand structure. Carbon- and nitrogen assimilation, respiration, biomass increase, and senescence are represented within tree compartments, canopy and soil layers, as well as cardinal directions. Changes in vertical and horizontal dimensions are based solely on produced biomass, which is distributed across the tree according to the effectivity of resource accumulation of its fractions, considering the rules of 'pipe-model theory' and 'functional balance' as secondary allocation paradigms. The resource-driven dimensional expansion, which determines the individual exposition to environmental conditions and resource availability, represents a major feedback mechanism to tree development and thus enables the simulation of long-term stand behavior.

The model is evaluated with data gathered from spruce and beech trees growing together at intensive-investigation sites in South-Germany. At these sites, spruce has performed an increase in competition strength relative to beech over several decades, probably due to nitrogen deposition, but shows a considerably larger sensitivity to drought. The model simulations demonstrate that an increase in the frequency of dry years will shift the competition conditions in favor to beech, but that spruce nevertheless might still grow better, depending on the degree of environmental change and silvicultural treatments.

Takashi Kohyama and Takuya Kubo

Population-level processes of overcrowded subalpine fir stands, reconstructed from a shoot-based simulator of tree architecture.

Density dependence of plant population processes has been analysed independently of ecophysiological processes. Recent evaluation demonstrated that size-distribution-based models of plant populations with one-sided competition along vertical canopy profile readily reconstructed density-yield relationship, self-thinning, and time trends of size distribution. However, when an individual is expressed by one size dimension (i.e. trunk diameter), such models cannot explain geometric scaling of self-thinning and allometric change with time.

We took an alternative, shoot-based approach to analyse the population-level consequence of density dependence. We constructed a simulator named "PipeTree" to describe annual shoot growth and branching of tree crowns in three-dimensional space. Constraints included were simple allometric relationship at current-year shoots, branching rule, pipe-model relationship that relates stem sectional area and the above foliage mass, available light resource at every shoot tip that controls foliage assimilation, and operational assimilate allocation rules. We tuned it to subalpine fir populations for quantitative validation.

We could reproduce the development of size hierarchy due to crowding, the geometric rule of self-thinning, and the time course of trunk diameter vs. tree height allometry, all observed in actual fir stands. Quantitative patterns of the density dependence of plant populations were therefore satisfactorily explained only by light-resource limitation in packed foliage distribution. We also predicted the population-level response to increasing atmospheric carbon dioxide. Resulted change was no mere acceleration of stand-level production, but was coupled with architectural modification of stand canopy.

Risto Sievänen, Pekka Nygren, Frank Berninger and Eero Nikinmaa

Coupling a transport/resistance model of allocation with a model of crown architecture

LIGNUM is a functional-structural model [1] that treats the 3D tree crown as an assemblage of elementary units that closely resemble the real structure of the tree. The available photosynthetic products, after respiration losses are accounted for, drive the growth of the tree. The photosynthetic production in an elementary unit depends on intercepted radiation and the respiration of the living biomass of the unit. During the time step of one year new units are added, the existing ones increase in size, and senescing elements are shed. The growth increments between the elementary units are divided using the pipe model and other principles governing the structure of trees. LIGNUM has been applied to e.g. Scots pine and sugar maple trees.

However, new applications of LIGNUM, such as study of seasonal variation in carbon allocation, require improving the corresponding model components. We have combined into LIGNUM an existing model of the dynamics and utilization of carbon and nitrogen substrates in a tree [2] (CNM). CNM considers both substrate and reserve carbon and nitrogen in the above-ground and below-ground parts. The transport between the compartments and utilization in growth of substrates is based on a modification of the transport/resistance approach [3]

In the combined model, LIGNUM and CNM have retained their basic features; they work together by exchanging data. LIGNUM evaluates rates of both photosynthesis and respiration that are used as input for CNM. CNM calculates in turn the mass of substrates used in growth in above- and below-ground parts, which information is fed into LIGNUM that converts the mass into changes of the 3D crown structure. The time step of LIGNUM has been shortened to correspond to the fraction of day of CNM. The combined model makes possible to study the interplay of the 3D crown structure and carbon and nitrogen dynamics in a tree.

The combined model has been parameterized to *Gliricidia sepium* (Jacq.) Walp. (Papilionaceae: Robinieae) growing as a shade tree in an agroforestry system in humid and subhumid tropical conditions. We present simulations and data on *Gliricidia sepium* trees under different pruning regimes.

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Veli-Pekka Ikonen, Heli Peltola and Seppo Kellomäki

Modelling the structural growth, stem and wood properties of Scots pine (*Pinus sylvestris* L.) related to silvicultural management with implications in simulated sawing

The modelling work of this study aims at linking together how different stem and wood properties in Scots pines (*Pinus sylvestris* L.) are related to silvicultural management. In the modelling, the three-dimensional structure of the tree is determined as affected by the local light conditions on shoots (which are basic computational units). The growth, death and pruning-off of shoots and branches are modelled over the life span of the tree using time step of one year, taking special care to identify the location of green and dead knots in the wood. The properties of the stem are further described in terms of the stem form, wood density, heartwood and sapwood, early and latewood and fiber length. Related to above work, a sawing simulator can be used to compute the properties and value of sawn boards for the simulated trees as related to silvicultural management. In this presentation, it will be demonstrated the ability of the model to produce a realistic crown and stem structure, and different wood properties such as average wood density, early and latewood percentage and fiber length within a tree. Furthermore, examples will be presented for the properties of sawn boards of simulated trees as related to silvicultural management.

Danielle J. Marceau

**Complex systems theory and forest dynamics :
What can we learn from the SORTIE model?**

Complex systems theory has emerged during the last decades through the development of innovative concepts such as chaos, fractals and dissipative structures to characterize the behavior of non-linear, open, adaptive systems. A complex system can be simply described as composed of a large number of components that interact with each other in a non-linear way and adapt through time. Complex systems are hierarchically structured and scale-related. The higher level of the hierarchy defines the set of constraints imposed upon the level of observation, while the inferior level represents the set of individuals composing the level under observation. According to complex systems theory, the global structure of a system emerges from the multiple local spatial interactions between individuals occurring through time within its constraint domain. Ecosystems, such as forests, are said to be complex due to the variety of interactions between their biotic and abiotic components, their self-organization property, and their capacity to adjust to disturbances to maintain their structure. Since top-down, deterministic models have been found to be poorly adapted to the study of complex systems, a new class of models was lately developed in attempts to capture and decipher the dynamics of such systems. Among these models is SORTIE, a northern hardwood forest succession model developed by Pacala and Canham in 1993, that simulates the growth, mortality and reproduction cycle of individual trees based on the quantity of light that reaches and penetrates the canopy. SORTIE offers three main characteristics for the study of forest complexity: it is object-oriented, individual based and spatially/temporally explicit. So far, the model was tested to study the impact of natural disturbances (gaps of various sizes, propagation of insect disease, and ice storms) and anthropic disturbances (selection cutting). More specifically, SORTIE was used to characterize the global spatio-temporal structure of gaps, to assess the volumetric light environment generated by small-scale disturbances and its impact on various tree species, and to simulate gap closing process.

The objectives of this paper are twofold. First, the most important ecological contributions provided by SORTIE will be described. These central questions will be answered: What new things did we learn from SORTIE about forest dynamics? How can this knowledge be used by scientists and forest managers? Second, key conceptual and methodological issues in relation to complex systems theory and the use of SORTIE will be addressed, such as: sensitivity to initial conditions, emergent structures and phase space solutions generated by the model, as well as the problem of calibration, validation and generality of such a model. The thesis advocated in this paper is that SORTIE offers an innovative way to explore scenarios and formulate new hypothesis about forest dynamics within the post-normal science paradigm.

André Ménard, Danielle J. Marceau, André Bouchard, Patrick Dubé and Charles D. Canham

Tree release episodes in the neighborhood of small-scale disturbances (SSD): a modeling assessment of SSD extent and impact

Small-scale disturbances (SSD) correspond to both forest management interventions and natural canopy gaps. They are recognized as a crucial component of eastern deciduous forest dynamics and can be applied by forest managers to promote forest growth. However, our understanding of SSD impact based on field studies is spatially and temporally limited. The spatial extent of such studies is restrained by the fastidious data collecting work it necessitates, while the temporal observation window rarely surpasses ten years. Also, they rarely focus on the outer part of canopy gaps, assuming that their impact is limited to the area defined by the vertical or the extended projection of the gap. However, under-canopy light regime and dendrochronological studies suggest that SSD impact expands significantly outside the traditional gap. This study aims at characterizing SSD impact on radial growth of neighboring trees with the forest succession simulation model SORTIE, a stochastic and mechanistic spatially-explicit individual-based model. Simulations were performed using SSD of different sizes that were introduced after 400 years. For all the trees (DBH > 2 cm) present at the SSD time of introduction, species-specific growth suppression and release values were used to determine their growth state and show the extent of the SSD impact. This study reveals the relationship between SSD sizes and multiple characteristics of the impact extent (intensity, orientation, species differential responses, etc). Such results bring new insights to the gap physical definition debate, and can be useful for forest manager's interventions.

Poster Session

Marilou Beaudet, Christian Messier and Charles D. Canham

Predictions of understory light conditions in northern hardwood stands following parameterization and tests of the SORTIE light model

In this study, we parameterized the light model of SORTIE for northern hardwoods in eastern Canada, and performed validation tests of the model before using it to predict the effect of various types of partial cutting on understory light conditions. The parameterization was done by characterizing the crown geometry and openness of sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.) and beech (*Fagus grandifolia* Ehrh.). Those results indicated that beech casted a deeper shade than sugar maple and yellow birch. Validation tests of the model were performed in both mapped and un-mapped plots by comparing light predicted by SORTIE to light measured in the field using hemispherical photographs and sensor-based measurements. In mapped stands, the model provided a reasonable prediction of the overall spatial variation in understory light levels between 2 and 30% full sunlight. Under 10% full sunlight, however, the predictions remained accurate but lacked spatial precision. In un-mapped stands, SORTIE accurately predicted stand-level mean light availability at 5 m aboveground for stands ranging in basal area from 19 to 27 m²/ha. At heights lower than 5 m, SORTIE accurately predicted the light availability in a recent selection cut with a low density of understory vegetation but tended to overestimate light availability in stands with relatively dense undergrowth. Finally, a demonstration of the possible usefulness of the SORTIE light model is presented by using the model to compare the proportion of various light microsites created by a variety of selection cutting systems in used in eastern Canada (selection cutting with different harvesting intensities, group selection, and patch selection).

Olevi Kull, Ingmar Tulva and Elina Vapaavuori

Consequences of elevated CO₂ and O₃ on birch canopy structure: implementation of the canopy growth model

Plant success in competition for resources depend strongly on the ability to increase number, sizes, and efficiency of modules through which resources are acquired (Pritchard et al. 1999). Therefore, besides the effects of changing environment on specific rates of acquiring resources, the effects on tree structure might be crucial to understand how competitive ability of a tree species and stand level production will change when CO₂ and O₃ concentrations in plant environment increase.

We are using canopy growth model by Kull & Tulva (2000), based on shoot growth and ramification information, to predict canopy level changes in foliage distribution in response to elevated CO₂ and O₃. Experimental data were collected within the open-top chamber study with *Betula pendula*. In this experiment two clones, one considered as ozone-sensitive and the other as ozone-tolerant, were exposed to elevated (ca 2x ambient) concentrations of O₃, CO₂ and CO₂xO₃. The two clones responded strongly but largely in opposite manner to the both altered factors. CO₂ tended to affect mainly ramification related parameters, whereas O₃ influenced more strongly shoot length and number of shoot nodes. A strong synergetic effect of O₃xCO₂ interaction appeared in vertical pattern of shoot length.

The model calculations showed that elevated CO₂ would affect the most strongly the canopy steady-state leaf area index (LAI). In the ozone-sensitive clone the steady state LAI will increase considerably under elevated CO₂ and this increase will be even amplified at simultaneous increase in ozone concentration. According to the model prediction, in this clone the changes in gaseous environment will change considerably the vertical distribution of foliage, shifting the maximum leaf area density towards the top of the canopy. The possible changes in spatial aggregation (clumping) of the foliage will be also discussed on basis of the model predictions.

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Kiyoshi Umeki

Effect of light intensity on the allocation of growth in young *Betula platyphylla* saplings

To develop functional-structural tree models, several dynamic processes must be modeled, which include spatial distribution of resources, resource acquisition by foliage or root, matter production in foliage, and allocation of growth. Among the above processes, the last process has been poorly understood. I quantified biomass increment of first-order (branches attached directly to the main trunk) branches and the main trunk in *Betula platyphylla* saplings, and examined the patterns of growth allocation to branches and the main trunk in relation to the light intensity and the position of the branches within an individual.

In 2000, I selected 25 naturally growing *Betula platyphylla* saplings (1.05 – 3.08 m in tree height) in a disturbed forest stand in Nakagawa, northern Hokkaido, Japan. After the full expansion of foliage, I took hemispherical photographs at the tip of every first-order branches in the selected saplings, and quantified relative PPFD from the photographs. The study site includes a large gap and a closed stand next to the gap; the maximum relative PPFD in each sapling ranged from 16.7 to 90.2 %. At the end of the growing season, I harvested the saplings, measured the diameter and length of every shoot in the saplings, and calculated the biomass growth that is allocated to current-year long shoots in each first-order branch. I also evaluated biomass growth allocated to the main trunks by measuring the tree rings.

Within each individual, growth allocation to current-year long shoots in a first-order branch did not have clear relationship with the relative PPFD of the branch and the product of the relative PPFD and the number of leaves (a surrogate variable for the amount of light captured by the branch). However, it had a fairly clear relationship with the vertical position of branches within an individual; growth allocation to long shoot concentrated in the upper part of individuals. At the individual level, the total growth allocated to current-year long shoot within an individual balanced well the growth allocated to the main trunk. These patterns suggested the control of growth allocation at the individual level.

Danilo Dragoni, A.N. Lakso and S.J. Riha

Approaches to modeling water fluxes through soil-plant-atmosphere continuum in an apple orchard.

Water status is an important factor in affecting growth, production, and health of apple trees. Moreover, it is important in defining the needs, economics and design of irrigation in orchards. Even in climates with adequate rainfall, drought periods can have serious impacts on apple production, and a model that integrates mechanisms regulating water uptake, transport and transpiration loss by apple tree would be useful to add a predictive component to the orchard management.

General mechanisms of water uptake, transport and transpiration, together with specific models of soil-plant-atmosphere continuum, are fairly common in literature. Nevertheless, those models cannot be directly applied to the apple tree system, since they do not deal with the specific characteristics of the apple trees in orchard (e.g. primarily, discontinuous canopy, and large extent, but low density root systems). Another important factor is the very high hydraulic internal flow resistance in the tree.

This work focuses initially on the atmosphere-canopy component of the water continuum. The approach used to model considers the orchard as two separate sub-systems, namely rows and alleyways. A description of the driving environmental variables (for instance net radiation and light interception) in term of the two different components is then necessary to describe the two sub-systems. Focusing on the tree component only, it is possible to describe the relationships among potential transpiration of an apple tree and environmental factors such as net radiation, water pressure deficit, and atmospheric turbulence conditions. This last factor, in particular, requires a dedicated approach because of the non-homogenous spatial distribution of the tree rows. A spatial model approach, considering the direction and intensity of the wind, has been adopted. Validation of this approach will be done with field measurements of the water use by sap flow methods over period of varying weather.

Yann Nouvellon, Saint-André, L., Dauzat, J., Roupsard, O., Caraglio, Y., Hamel, O., Berbigier, P., Bonnefond, J-M., Irvine, M., Mabilia, A., Epron, D., Mouvondy, W., Laclau, J-P., Bouillet, J-P., Jourdan, C.

Linking tree architecture and function for continuous simulations of carbon, water and energy fluxes from Eucalyptus stands in Congo

By accounting for both the structural and physiological properties of plant stands, functional-structural models are powerful tools to investigate plant-environment interactions. On the other hand, due to the detailed description of plant architecture, they are generally computationally heavy and difficult to apply over long period of time. The objective of this study was to combine a multi-layered soil-vegetation-atmosphere (SVAT) model with simulation modules working on 3D plant models, to perform continuous simulations of gas and energy exchanges, and tree growth in clonal Eucalyptus stands.

First, short-wave radiative transfers are simulated on 3D plant models at a 30-minute time step, using MIR, MUSC, and RADBAL models. The radiative balance and structural parameters computed for the different scene components are subsequently used as input in a multi-source, multi-layered SVAT model to simulate, with the same time step, sensible and latent heat fluxes from the trees and the understory, radiative transfers in the thermal-infrared domain, root water uptake, temperature and moisture dynamics in the soil and the canopy, photosynthesis and plant organ respiration. Heterotrophic soil respiration is computed empirically from simulated soil moisture and temperature profiles. Variables such as leaf and root water potential, stomatal conductance, and component temperatures, are estimated by iterative procedures. Finally, simulated plant carbon budgets are used to modulate tree growth within the computerized Eucalyptus stands.

The simplification of the canopy structure used to compute gas exchanges made this 'hybrid-model' computationally applicable over large stands and long period of time, but brought with the difficulty of estimating the 'effective' value of several parameters. Effective parameter values were determined by comparing the simulations obtained from the hybrid-model in various meteorological conditions with the simulations obtained from a structural-functional tree and stand (FSTS) model that simulates stand fluxes by integration of the fluxes computed at the leaf level. The hybrid-model was then applied on a 2.5 year-old Eucalyptus stand in the Congo, using soil texture and meteorological measurements. Continuous simulations performed over a 6 month period were compared for validation purpose with measurements of sap fluxes, soil water content and temperature profiles, tree growth, and measurements of latent and sensible heat, and CO₂ fluxes obtained during the same period with an eddy-correlation system.

Rüdiger Grote

A model for simulation of long-term competition effects in mixed forests

A new tree growth model (BALANCE), which considers crown expansion from the outcome of physiological processes, is presented. The processes are driven by individual environmental conditions, including climate, deposition, and air chemistry, which are estimated from field conditions and stand structure. Carbon- and nitrogen assimilation, respiration, biomass increase, and senescence are represented within tree compartments, canopy and soil layers, as well as cardinal directions. Changes in vertical and horizontal dimensions are based solely on produced biomass, which is distributed across the tree according to the effectivity of resource accumulation of its fractions, considering the rules of 'pipe-model theory' and 'functional balance' as secondary allocation paradigms. The resource-driven dimensional expansion, which determines the individual exposition to environmental conditions and resource availability, represents a major feedback mechanism to tree development and thus enables the simulation of long-term stand behavior.

The model is evaluated with data gathered from spruce and beech trees growing together at intensive-investigation sites in South-Germany. At these sites, spruce has performed an increase in competition strength relative to beech over several decades, probably due to nitrogen deposition, but shows a considerably larger sensitivity to drought. The model simulations demonstrate that an increase in the frequency of dry years will shift the competition conditions in favor to beech, but that spruce nevertheless might still grow better, depending on the degree of environmental change and silvicultural treatments.

Kenji Seiwa, Takahiro Kadowaki, Sigetoshi Akasaka, and Kihachiro Kikuzawa

Shoot life-span in relation to successional status for 15 deciduous broad-leaved tree species

In tree species, leaf life-span is closely related to environmental conditions of the habitat or successional status. Early successional species in abundant resource (light, nutrient) conditions usually shows shorter leaf life-span compared with late-successional species in poor resource conditions. In temperate deciduous broad-leaved trees, since most of the leaves attach to current-year shoots, investigation of life-span of the current-year shoots would reveal the more precise linkage between the light acquisition mechanisms and their habitat conditions. We monitored shoot survival during the period of 3 growing seasons for 15 species (3 families), which have a wide range of successional status.

Among 6 species in Salicaceae, *Salix jessoensis*, *S.sachalinensis* growing in resource (light, water, and nutrient) rich habitats such as flood-plain and riverside shed more than 75 % of the current-year shoots until the end of first growing season, resulted in short shoot life-span. In contrast, *Salix vulpina*, *Populus maximoviczii* growing in a wide range of habitats including resource poor sites such as hill slopes and ridge retained most of the current-year shoots until the end of first growing season but shed all the shoots until the end of 3rd growing season, resulted in longer shoot life-span. In Fagaceae (5 species) and Betulaceae (4 species), similar negative relationships between shoot life-span and productivity of the habitat were also observed, although the extent was different.

Shoot life-span was also closely associated with shoot architecture (size hierarchy and the arrangement of current-year shoots on a 1-year shoot). Analysis of the linkage among shoot life-span, shoot architecture and habitat productivity may be important to reveal the optimal resource acquiring behavior in hardwood species.

Naoto Ueno and Kenji Seiwa

Intersexual differences in shoot architecture and functions in a dioecious tree, *Salix sachalinensis*

In dioecious plants, females are believed to pay greater reproductive cost compared with males due to seed production. To reveal how do females compensate for the cost, we investigated intersexual difference in architecture and functions of shoots in a dioecious tree, *Salix sachalinensis* in a riparian forest, northern Japan. In the early growing season, females produced a greater number of vegetative shoots compared with reproductive shoots. In males, the reverse was true. And then, females shed a greater number of vegetative shoots than males until the end of growing season, resulted in little difference in the number of vegetative shoots between sexes. Vegetative shoots in proximal positions of 1-yr shoots shed most frequently, while most of the vegetative shoots in the terminal positions survived until the end of the growing season. This trait suggests that short-lived vegetative shoots can utilise the available space entirely even in proximal position of the shoots in which abundant light is available only in the early spring. In females, greater and earlier investment of resources to leaves (vegetative shoots) enhances the photosynthetic activity during the flowering and seed maturing stages in spring, indicating their compensation mechanism for the reproductive cost. Analogous to seedling RGR analysis, all of the RGR components of vegetative shoots, leaf N contents, SLA, LWR and LAR were greater for females than males, but not significant for SLA. In females, their superior architectural, morphological and physiological shoot functions are considered as the compensation mechanisms for their greater reproductive cost.

Frédéric Raulier, Pierre-Yves Bernier, Chhun-Huor Ung, Richard Fournier, Luc Guindon and Jacques Régnière

Error estimation on net primary productivity predictions at the landscape level in the boreal forest of Eastern Canada.

Modelling NPP over large landscapes requires spatial inputs of reasonable quality, but error in input estimation produce error in predicted NPP over and above of the error caused by misrepresentation of processes within the model. Both sources of errors are evaluated in the present modelling and validation exercise. The model used is StandLEAP, a modified version of 3PG (Landsberg and Waring, 1997, For. Ecol. Manag. 95: 3, 209-228) that takes into account the strong seasonality of forest growth at Northern latitudes. The net primary productivity (NPP) is modeled across a 2,400 km² region of boreal and sub-boreal forest north of Québec City, Canada. Modelling is performed on 30x30m pixels for the whole landscape. The validation is based on sixty field plots established throughout the region. Three different estimates of total NPP (above and below-ground) are obtained for each plot. The first is derived directly from the actual field measurements of tree diameter increments and soil cores. The second is derived from the application of StandLEAP to each plot, using the appropriate plot data on stand properties as input. The third is obtained from the full spatial application of StandLEAP to the complete region using the spatial data of stand properties derived from satellite remote sensing and stand maps, and the extraction of NPP from the resulting map using plot coordinates. The effect of the sampling strategy used to estimate NPP on these plots is first evaluated. The error associated with the model predictions is estimated by comparing field measurements of NPP to modelled estimates using plot data. Finally, the error associated with the use of spatial data is estimated by comparing modelled NPP modelled using plot data to NPP obtained from spatial application of the model.

André Lacointe

Rendering the effect of source-sink distances in whole plant carbon partitioning models

Among current whole-plant C partitioning models¹, the most mechanistic are transport-resistance models, which give a simplified representation of the Münch mass flow transport process. In particular, they account for a major feature of assimilate allocation in large plants: the negative effect of relative source-sink distances on allocation coefficients. However, due to the difficulty of estimating their parameters, their practical use has been very limited. Instead, a number of models designed for particular species compute the internal C fluxes as depending both on the amount of assimilates available at the whole plant level and on the respective C demand or potential growth of individual sink organs (« sink strength »), either in a proportional or in a hierarchical way. In these models, source-sink spatial relationships are not taken into account (or very roughly in some hierarchical models, as the priority levels of different sinks)¹.

The present work was intended to extend proportional models with an explicit though simple modulation of the C fluxes by the source-sink distances, without requiring the estimation of concentration gradients or solving complex equation systems. Thus, the allocation coefficient between source #i and sink #j is expressed as:

$$\lambda_{ij} = \frac{D_j \cdot f(d_{ij})}{\sum_{k: \text{all sinks}} [D_k \cdot f(d_{ik})]}$$

where D_j is the C demand of sink #j (this « sink strength » is merely local, which is not the case in classical proportional models), and $f(d_{ij})$ a decreasing function of the metric distance d_{ij} between source #i and sink #j.

Two forms were tested for function f : $f(d_{ij}) = e^{-r \cdot d_{ij}}$ and $f(d_{ij}) = (b + r \cdot d_{ij})^{-a}$.

Function parameters and C demands were estimated by non-linear fitting of λ_{ij} coefficients derived from the very detailed dataset used by the empirical model ECOPHYS², which provides both experimental allocation coefficients and architectural/metric data obtained on young poplar³. In order to avoid phyllotaxy effects and improve consistency among sinks, individual leaf or internode sinks of similar characteristics were joined together, resulting in a total of 5 sinks. Distance d_{ij} was computed as the average distance between source #i and all individual components of sink #j.

The effect of distance was highly significant, *i.e.* both forms of f yielded a much better fit than when spatial relationships were ignored ($f = \text{constant}$, original proportional model). Both exponential and power forms yielded similar results. In both cases, the goodness of fit was significantly improved if different values for parameter r were allowed for different stem segments.

Thus, the $f(d_{ij})$ extension of proportional models can simulate fairly well the effect of spatial relationships on C allocation as described by the ECOPHYS dataset. However, it has still to be tested in different situation, e.g. in plants of different architecture or size. In this respect, the power model (with different resistivities) may be a better choice than the exponential due to its slower rate of change with d_{ij} .

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Christiane Eschenbach

**Validation of the photosynthesis module of ALMIS
at leaf, shoot and whole tree level**

Functional-structural tree models, which link tree physiology and architecture provide a useful tool to describe and study the long-term effects of single ecophysiological processes on whole plant growth. Our tree growth model ALMIS is based on an object-oriented approach and uses a modular representation for each tree. The model development and parameterization are based on data from extensive field investigations of an alder forest (*Alnus glutinosa*) in the Bornhoeved Lakes Region, Northern Germany. Among the various procedures, which are employed to model carbon and nutrient uptake and matter fluxes between the plant organs, the processes of carbon gain are of crucial importance.

In the present study, different methods were used to validate the photosynthesis module at different temporal and spatial scales. Net photosynthesis (photosynthesis minus dark respiration) of the leaves depends on their ambient microclimatic conditions (PPFD, T, VPD), and the leaves respond differently to a given factor due to differences in seasonal and spatial acclimation. Modelling of canopy photosynthesis takes foliage area (LAI, LAD) and its varying sun-lit and shaded proportions into account and is based on microclimatic conditions measured at different levels within the canopy.

At different scales the model output was compared with results of direct measurements. These included measurements of leaf gas exchange, investigations of biomass dynamics, and analysis of tree-rings. Comparison of modelled and independent measured diurnal courses of leaf gas exchange showed a very good agreement. The amount of biomass generated in a representative crown compartment during different months was found to be correlated to the estimated respective amount of assimilates gained during the same periods. Finally, carbon gain of the alder trees was modelled for the years 1990-1995 on the base of continuously measured microclimatic conditions. The annual net assimilation rates showed a strong linear relationship with stem increase of the respective years. Thus, the photosynthesis module is proved to be qualified and can be adopted to the ALMIS model.

Daniel Mailly, Sylvain Turbis, Stéphane Poirier and Richard Fournier

Influence of crown shape and distribution on light interception: application of a light model and implications for stand-level modelling

Light is generally considered the most important resource in forest simulation models. Traditionally, it has been computed using the Beer-Lambert law, but more sophisticated approaches integrating spatial components and ray tracing algorithms are being used and developed today. Although these new approaches take into account several factors such as leaf area density, crown radius, crown depth, foliage inclination and ray sample size, very little attention has been given to the exact influence of crown shape on light calculations. In order to study the influence of crown shape on light calculations, we tested various crown shapes such as cones, ellipsoids, cylinders, paraboloids, hyperboloids, and superellipsoids. Using these crown shapes, we produced and analysed hemispherical images of actual stem-mapped black spruce stands using a light model and a ray tracing program. Results will be discussed in terms of the implications of selecting a particular crown shape for light calculations in forest stand models.

Sylvain Turbis and Daniel Mailly

**OpenGL and PovRay as powerful tools to visualize and analyse
stand structure in a forest simulation model**

OpenGL and PovRay can be very powerful tools for visualizing trees in a simulated forest stand. These tools allow the stand to be viewed from different angles and with different levels of lighting. Crowns and trunks of various shapes, textures, and colors can be associated with each tree species. The resulting images can be transformed into fisheye images and analysed in order to compute canopy structure and light indices. In this poster we will present how these tools can assist forest modellers in extracting and using information from stem-mapped stands.

Karin Rebel and S. J. Riha

A Spatial Explicit Model of Water Uptake by Trees in a Watershed

A simple, spatial, 3-dimensional, dynamic model of water uptake by trees in a watershed was developed using the PCRaster Dynamic Modeling Package. This software provides a computer language especially developed for modeling temporal and spatial processes in a GIS, and is well suited for the development of dynamic ecological and hydrological models.

The model we developed is grid based and has vertical layering. The water budget is calculated for each grid cell in every layer for every time step. Change in soil water storage is obtained by adding the incoming water and subtracting the outgoing water in each grid cell soil layer. When a soil layer in a grid cell exceeds field capacity, water can potentially flow to the grid cell in the layer underneath. However, when soil water reaches saturation, water can flow to the grid in the direction of the local drainage. Potential evapotranspiration sets the upper limit of water uptake in this model. Actual transpiration falls below potential evapotranspiration as soil water content approaches the permanent wilting point. The spatial distribution of the water budget components is available for every time step.

We are using this model to simulate water uptake and subsurface lateral movement in a coniferous and a mixed hardwood - coniferous forest on Coastal Plain soils of the southern United States. These soils are characteristically sand overlying slowly permeable clays found at depths of 30 to 200 cm. Temporary perched water tables can develop. We use this model to evaluate the impact of these temporary water tables on tree water uptake, through their impact on rooting depth and plant available water.

Erwin Dreyer, Pierre Montpied, Sylvain Delagrance, Piotr Robakowski, Delphine Retzinger, Pierre Dizengremel, François Alain Daudet, Xavier Leroux

Parametrisation of leaf photosynthesis models in seedlings from a range of broadleaved tree species grown under diverse irradiance microclimates.

Modelling carbon assimilation requires access to primary data describing photosynthetic capacity at leaf level under a range of environmental conditions. This can be achieved basing on a widely used semi-mechanistic leaf photosynthesis model that includes three main processes : interception of irradiance by Light Harvesting Complexes, light driven electron fluxes, and RuBP-carboxylation rates ('Farquhar" model). Maximal carboxylation velocity (V_{cmax}) and maximal light driven electron flow (J_{max}) can be adjusted on response curves of net assimilation rate (A) vs intercellular partial pressure of CO_2 (c_i). This approach was applied to seedlings from a range of broadleaved and coniferous tree species grown under different irradiance microclimates (full sun, 48, 18 and 8 % incident PFD, in a nursery at Champenoux, North Eastern France) and in a beech stand. It was used to analyse i. the temperature response of V_{cmax} and J_{max} ; ii. the response to irradiance in relation to leaf structure (leaf nitrogen in particular); iii. the seasonal course of photosynthetic capacity in a *Fagus sylvatica* stand. Main results were: i. thermal optima ranged from 32 to 35°C for J_{max} , with significant differences among species, and from 36 to above 40°C for V_{cmax} ; ii. large differences were recorded in photosynthetic capacity among species, with in particular significant differences in the $J_{\text{max}}/V_{\text{cmax}}$ ratio; iii photosynthetic capacity increased with irradiance, with a constancy of the $J_{\text{max}}/V_{\text{cmax}}$ ratio. From these data we computed the fraction leaf nitrogen invested in bioenergetics, in Calvin cycle enzymes and in light interception. The first two were rather stable with irradiance, but differed largely among species; while the third varied both with irradiance and species. Data from seasonal time courses are still under processing. The main conclusion is that leaf structure, including nitrogen, varies with irradiance, and that photosynthetic parameters at leaf level vary largely independently of leaf nitrogen. This variability needs to be documented in order to base photosynthesis models on a sound basis at a large time scale and under a wide range of environmental conditions.

Manfred Küppers, Ralf List & **Christiane Eschenbach**

MADEIRA:

Simulating Environmentally Sensitive Growth of Canopy Architecture as Based on Woody Plant Physiology and Morphology – Examples and Applications

MADEIRA is based on the metamerism growth pattern of woody plants employing a seasons's twig axis as a modular basis. Therefore, a simulated plant is the result of the „sum“ of all modules' characteristics, and its form implicitly contains its growth history, as is the case in nature. For environmentally sensitive development the model employs a minimum of exclusively measured biological information, such as absorption of light in the growing canopy, annual carbon gain by leaves, balances of assimilate fluxes into branches, stems, roots and leaves and species-specific branching patterns together with frequencies. From these it simulates biomass increment (length and thickness) of every individual twig axis as driven by the assimilate flux into it either from a neighbouring (leafless) twig or from photosynthetic carbon gain by its own leaves, always knowing its leaf area, number and biomass, respiration, age etc..

The model successfully simulates canopy architectural development. For example, exchanging branching patterns results in different growth forms already after a few vegetation periods of growth. Trees and shrubs can be „driven“ by their appropriate or by different physiologies during competition for light and even at early stages of successional replacements of species. Furthermore, MADEIRA allows for tests of sensitivity in growth and architectural development: E.g., making a species to grow at a ten-fold annual carbon gain of its sun leaves, maintaining all other parameters (like light absorption by the canopy) identical, still results in less height gain as compared to a competing species growing at „normal“ carbon gain, if the branching characteristics are not appropriate. Thus, such models allow to check for the relative importance of physiology versus morphology in competitive situations just by exchanging (in the simulation) the „genome“ driving relevant subprocesses among species. Principally, after further improvement, they allow to study long-term effects such as global warming and rise in carbon dioxide on species growth and many others.

Belinda Medlyn, Paul Berbigier, Achim Grelle, Denis Loustau & Sune Linder

Two Contrasting Flux Sites Used To Test A Model Of Forest Canopy Gas Exchange

Modellers have welcomed the development of eddy-flux measurement technology because of its potential for fine-scale testing of models of forest growth. However, one limitation to testing models against flux data from a single site is the observational, rather than experimental, nature of these studies, which restricts our ability to test the mechanisms incorporated in models. This limitation can to some extent be overcome by testing models against flux data from two or more contrasting sites.

In this study, we tested the MAESTRA model against flux data from two coniferous forests growing in contrasting climatic conditions: Bray, a temperate pine forest in southern France, and Flakaliden, a boreal spruce forest in northern Sweden. The model was parameterised from detailed ecophysiological measurements made at each site. Leaf area index was similar at the two sites. Leaf-scale photosynthesis and stomatal conductance parameters were lower at Flakaliden, but respiration rates were comparable.

Measured net ecosystem C uptake at Bray is considerably higher than that at Flakaliden (1997 values: 4.3 and 1.9 t C ha⁻¹ yr⁻¹, respectively). The model predicted a similar difference in NEE. According to the model, the primary reason for the difference between sites was the low incident radiation and temperature at Flakaliden, which act to reduce photosynthetic uptake, while a secondary reason was the lower leaf photosynthetic rates at Flakaliden. Using fine-scale testing of the model against flux data, we were able to confirm that these two factors were the main reasons for the difference in ecosystem C uptake between the sites.

Pepper, D.A., **McMurtrie, R.E.**, Medlyn, B.M., Owensby, C.E. and Linder, S.

Carbon sink responses of grassland and forest ecosystems to increasing atmospheric CO₂ concentration, rising temperature and increasing nitrogen fixation

The terrestrial biosphere is currently thought to constitute a carbon (C) sink of approximately 2 Gt C yr⁻¹, representing some 25% of total anthropogenic C emissions. Concern that this sink could saturate, and exacerbate the rate of increase of atmospheric CO₂, has led to a concentrated effort to model its future course.

The response of the C sink to increasing [CO₂], atmospheric CO₂ concentration, and temperature is highly uncertain. It is possible that responses of various plant ecosystems will differ markedly. We simulate net ecosystem production (NEP) for three contrasting ecosystems (Norway spruce forest at Flakaliden in northern Sweden, *Pinus radiata* forest at the BFG site in south-eastern Australia and a tall-grass prairie in Kansas, USA), using a model of C and N dynamics in plant and soil (G'DAY). Simulations include scenarios with gradually increasing CO₂, temperature and N fixation over the next century.

Simulations were initialised by first running G'DAY to equilibrium at which NEP is zero. Effects of increasing temperature differed across the ecosystems, simulations showing negative NEP for the water-limited Kansas grassland, but positive NEP for both the nitrogen (N)-limited spruce and the N- and water-limited pine forests. The increase in C storage at the forests is a consequence of increased N mineralisation leading to an increase in wood C that greatly exceeds the loss of soil C caused by increased heterotrophic respiration. Under increasing [CO₂] treatments, simulations indicate that NEP reaches a peak within two to three decades at all three sites. Under increasing [CO₂] and temperature, however, our simulations show evidence of sink saturation at the Kansas site, but a sustained C sink over 100 years at both forest sites. The effect of N addition is larger (relatively) at the cool Flakaliden site and temperate BFG site than in Kansas. Responses to the three environmental variables are generally additive. The forest simulations are in contrast to recent claims that the terrestrial C sink will decline over future decades.