# Process-based, Spatially-explicit Modelling of Riparian Forest Dynamics in Central Europe – Tool for Decision-making in River Restoration

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# SUMMARY

During the last decades public awareness of the limitations of traditional engineering practices and the imperative to conserve nature have led to changes in river management; including river restoration measures. The enlargement of the fluvial corridor is one of the often considered management measures. However, the high-pressure on land-use, the conflict of interests, as well as the uncertainty of vegetation and landscape development scenarios after restoration, can make their implementation difficult. In actual decision-making processes of large river restoration projects, no dynamic long-term modelling approach of potential riparian woody species development exists mainly due to the complexity of interacting driving-processes creating lateral and longitudinal gradients. So far, forest succession models applied to riparian areas are not conceived for river areas found in Central Europe and do not address explicitly environmental influences like nitrogen scarcity or drought stress important for certain riparian systems, nor they cover integrally the vegetation-hydraulics interaction. To support and enhance the decision-making processes in river restoration projects and to provide a better understanding of riparian forest dynamics and its driving-processes, the present thesis develops a coupled model of ecological and hydraulic processes to simulate riparian forest dynamics for Central European conditions, particularly for the case of enlarged fluvial corridors. The developed model RIFOD ('RIparian FOrest Dynamics') – a distribution-based forest succession model (*i.e.* ecological model) coupled to a quasi-2D hydraulic model – simulates short or long-term riparian forest dynamics at a yearly time step. The model, applied on a 10 times 10 m mesh grid, is spatially-explicit concerning the interactions of the ecological and hydraulic processes and integrates 65 Central European tree and shrub species. The ecological model is based on developments of different upland forest succession models, which were improved, adapted and complemented in regard to the ecological processes in riparian areas, for example concerning regeneration, nitrogen dynamics, soil water availability or flooding stress. At the basis of the modelling of physiological flooding stress response of plants, we carried out an in-depth review of the actual knowledge of the flooding stress response of Central European tree and shrub species. The review could highlight the main biotic and abiotic factors that influence species response and revealed the broad but still vague knowledge about physiological mechanisms and species-specific data of plant response. Based on the above findings, the fuzzy set theory was chosen to model flooding stress response integrating the main abiotic factors (*e.g.* flooding duration, -depth). The Central European tree and shrub species

were classified into flooding tolerance classes by use of clustering analysis based on proxy-data, which allowed us considering indirectly the anatomical, morphological or physiological adaptations to flooding. To model mechanical flooding stress, existing mechanistic models simulating failure resistance to uprooting or stem breakage conceived for wind load studies have been adapted to the case of water flow. Required geometrical characteristics of trees and shrubs, such as crown width and crown heights, were estimated based on available field data, whereas rooting depths in dependence of the growth stage of an individual plant were simulated by developing a quasi-mechanistic vertical root growth model for Central European tree and shrub species. This root growth model allowed also a more realistic simulation of drought stress by calculating root water extraction in relation to the development stage of stand and determining species-specific and development dependent accessibility to groundwater – not integrated in the soil water balance so far. Compared to the situation in uplands, a more realistic modelling of nitrogen availability in riparian areas could be achieved by considering the loss of nitrogen via denitrifcation, as well as the loss of litter due to flooding. In opposition to existing riparian forest succession models, RIFOD considers riparian vegetation not as a purely dependent variable of flooding. Floods may affect vegetation but they are also affected by it, owing to the contribution of vegetation to hydraulic roughness. The coupling of the forest succession model to a quasi 2-D hydraulic model allowed considering this. Moreover, the quasi steady-state model approach allowed emphasizing on the ecological relevant lateral dimension and to make the model spatially explicit in the sense of vegetation-hydraulics interaction.

The current version of RIFOD finds its application in riparian areas in which the geomorphological activity of the river is not a dominant process or in case of restoration projects, for widened fluvial corridors with morphologically stable stream channels. Model evaluation (validation and sensitivity analysis) revealed that RIFOD simulates plausibly the ecological gradients observed in the field and the resulting riparian forest dynamics. By applying the model at different lateral fluvial corridor designs at the River Rhone, the consequences of a restoration measure and the change of the hydrological regime for woody vegetation could be illustrated. From a management point of view, the model revealed for example that relative benefits become smaller as the width increases or that in absence of morphological activity (*e.g.* lateral bank erosion) the hydraulic processes alone are not sufficient for reinitiating riparian forest succession even for high energy streams such as the River Rhone. Moreover, the model allowed verifying and discussing current scientific concepts and hypotheses, as for example the intermediate stress hypothesis. Simulation results revealed that biological diversity is highest between the very low

and very severe flooding stress levels confirming the intermediate stress hypothesis involving a trade-off between competitive dominant species which monopolise stable habitats and the few fugitive species that survive high levels of instability.

The value of RIFOD relies in the capacity of displaying tendencies of riparian forest dynamics and associated characteristics in function of different fluvial corridor design variants. Moreover, it allows the understanding of processes and patterns in nature by allowing exploring the consequences of a set of explicitly stated assumptions that are too complex to explore by other methods. RIFOD is the first process-based riparian forest dynamics model for Central Europe and can be seen as a step forward into a more integral modelling of the riparian forest dynamics and its processes in view of a decision-aiding tool for large river restoration projects. A future integration of geomorphological processes will allow the application of RIFOD to quasi-natural river conditions.

# KURZFASSUNG

In den letzten Jahrzehnten unterlag der Flussbau einem grossen Wandel. Verheerende Hochwasserereignisse und ein zunehmendes Natur- und Umweltschutzbewusstsein haben die Probleme des traditionellen Flussbaus aufgezeigt. Dem modernen Flussbau stellt sich eine neue Herausforderung: die Revitalisierung der Fliessgewässer bei gleichzeitigem Schutz vor Hochwasser – die Flussraumaufweitung ist eine der häufig angestrebten Flussbaumassnahmen. Landdruck, Interessenkonflikte, und Ungewissheit über Vegetations- und Landschaftsentwicklung nach einer Revitalisierung erschweren jedoch oft eine praktische Umsetzung. Die Gestaltung der Flussraumaufweitung und die damit verbundenen ökologischen Werte (z.B. Entwicklung von Auenwald) spielen daher im Entscheidungsfindungsprozess eine wesentliche Rolle. In letzteren wurden bis anhin keine Modelle beigezogen, welche eine langfristige und dynamische Modellierung der Auenwaldynamik bei verschiedenen Flussraumgestaltungen erlauben würden. Dies kann hauptsächlich auf die Komplexität der in Auengebieten vorherrschenden Prozesse zurückgeführt werden. Bestehende Auenwaldsukzessionsmodelle sind leider nicht für die Bedingungen in Mitteleuropa konzipiert und tragen den in Überschwemmungsgebieten bedeutenden Umwelteinflüssen wie beispielsweise Stickstoffmangel, zeitweiliger Wassermangel, Stress durch Hochwasser und auch den Wechselwirkungen von ökologischen und hydraulischen Prozessen zu wenig Rechnung. Um Entscheidungsfindungsprozesse zu unterstützen und das Verständnis der Auenwalddynamik und der verantwortlichen Faktoren zu verbessern, wurde in diesem Forschungsprojekt ein Modell entwickelt, welches die Auenwald-dynamik für die Bedingungen in Mitteleuropa simuliert, insbesondere für den Fall von Flussraumaufweitungen. Das entwickelte Modell RIFOD (‚RIparian FOrest Dynamics') ist ein verteilungsbasiertes Waldsukzessionsmodell gekoppelt mit einem quasi-2D hydraulischen Modell und simuliert die kurz- und langfristige Auenwald-dynamik. Das Modell ist räumlich-explizit betreffend der Wechselwirkungen von ökologischen und hydraulischen Prozessen und integriert 65 Mitteleuropäische Strauch- und Baumarten. RIFOD basiert auf Entwicklungen bestehender Waldsukzessionsmodelle, welche auf der Prozessebene verbessert und bezüglich den in Auengebieten vorherrschenden ökologischen Gradienten angepasst und mit neuen Prozessen ergänzt wurden. Im Vorfeld der Modellierung des physiologischen Stresses von Gehölzen durch Hochwasser, hat man eine eingehende Analyse des aktuellen Wissenstandes über die Auswirkung von Hochwasser auf die Mittel-

europäischen Baum- und Straucharten durchgeführt. Diese konnte die bedeutendsten biotischen wie abiotischen Schlüsselfaktoren, sowie die breite aber stets noch vage Kenntnis der physiologischen Prozesse und artspezifische Sensibilität hervorheben. Aufgrund dieser Erkenntnisse wurde der physiologische Stress durch Hochwasser, in Berücksichtigung der abiotischen Faktoren (z.B. Hochwasserdauer, -höhe), mittels Fuzzy Logik simuliert. Die Gruppierung der Baum- und Straucharten in Hochwassertoleranzklassen mittels Clustering, erlaubte den Einbezug der anatomischen, morphologischen und physiologischen Anpassungen dieser Arten. Der mechanische Stress durch Hochwasser, wie Stammbruch oder Entwurzelung, wurde durch die Anpassung bestehender für Windlast konzipierter prozessbasierter Modelle an Wasserzugkraft simuliert. Die notwendigen geometrischen Parameter der einzelnen Gehölzarten, wie Kronenlänge und -breite, hat man auf der Basis verfügbarer Daten geschätzt, wobei die Wurzeltiefen in Abhängigkeit des Entwicklungstandes eines Gehölzes durch ein neuentwickeltes, quasi-prozessbasiertes Wurzelwachstumsmodells simuliert wurden. Dieses Wurzel- wachstumsmodell erlaubte zudem eine realistischere Simulation der Wasser- verfügbarkeit. Dies einerseits durch die Berechung des Wurzelwasserentzugs in Abhängigkeit der Entwicklung des Auenwaldbestandes und andererseits durch die art- und entwicklungsspezifische Simulation der Grundwassererreichbarkeit. Grundwasser ist bis anhin im Wasserhaushaltsmodell nicht berücksichtigt worden. Durch die Simulation der Denitrifikation, d.h. dem Verlust von Stickstoff unter anaeroben Bedingungen, konnte den Prozessen in Überschwemmungsgebieten entsprochen werden. Die Vegetation steht aufgrund der Vegetationsrauhigkeit in enger Wechselwirkung mit dem Wasserabfluss, insbesondere durch die Verminderung der Fliessgeschwindigkeit und die daraus resultierende Erhöhung des Wasserstandes. Dieser Prozess wird bei den herkömmlichen Auenwaldsukzessions- modellen nicht simuliert. Die Kopplung des angepassten Waldsukzessionsmodells mit einem quasi-2D hydraulischen Modell erlaubt RIFOD diese Wechselwirkung zu berücksichtigen, zudem konnte man durch den quasi-stationären 2-D Modellansatz das Schwergewicht auf die laterale Dimension legen und die räumlich-explizite Wechselwirkung gewährleisten.

Das Modell RIFOD findet seine Anwendung in Überschwemmungsgebieten mit geringer geomorphologischer Aktivität oder im Falle von Revitalisierungsprojekten, für Flussraumaufweitungen mit stabilem Flussraumprofil. Die Modellevaluation zeigte auf, dass RIFOD die ökologischen Gradienten sowie die daraus resultierende Auenwalddynamik realistisch wiedergeben kann. Durch die Anwendung des Modells an verschiedenen Flussraumprofilen der Rhone konnten die ökologischen Folgen von Revitalisierungsmassnahmen oder von Abflussveränderungen in Bezug auf die

Gehölzvegetation aufgezeigt werden. Zudem erlaubte es, aktuelle wissenschaftliche Konzepte und Hypothesen zu diskutieren. Die Bedeutung von RIFOD liegt darin, dass es Tendenzen der Auenwaldentwicklung und der damit assoziierten Charakteristika bei veränderbaren Flussraumprofilen aufzeigen kann und damit zu einem besseren Verständnis für die in den Flusssystemen ablaufenden Prozesse führt. RIFOD ist das erste prozessbasierte Auenwalddynamikmodell für mitteleuropäische Verhältnisse und stellt einen weiteren Schritt in Richtung Entwicklung eines Hilfsmittels zur Entscheidungsfindung für Flussrevitalisierungsprojekte dar. Eine zukünftige Integration von geomorphologischen Prozessen erlaubt die Anwendung des Modells für naturnahe Flusssysteme.

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CURRICULUM VITAE

# CHAPTER 1

## General introduction

Riparian landscapes have unique environmental values, as they are considered as a terrestrial habitat, which is strongly affecting and affected by aquatic environments (Malanson, 1993). The interactions of ecological, hydraulic and geomorphologic processes create lateral and longitudinal gradients, which directly have an effect on structure, composition and dynamics of riparian vegetation communities. Particularly riparian forests maintain generally high levels of biodiversity (in various stages of succession), exhibit high rates of nutrient cycling and productivity and provide specialized ecological functions, *e.g.* the improvement of water quality. As the linear spatial configuration of riparian forests increases the interactions of the riparian zones with surrounding ecosystems, they are also of primer importance from a landscape-ecological point of view (Gregory *et al.*, 1991).

Ecological processes



Hydraulic processes

Geomorphologic processes
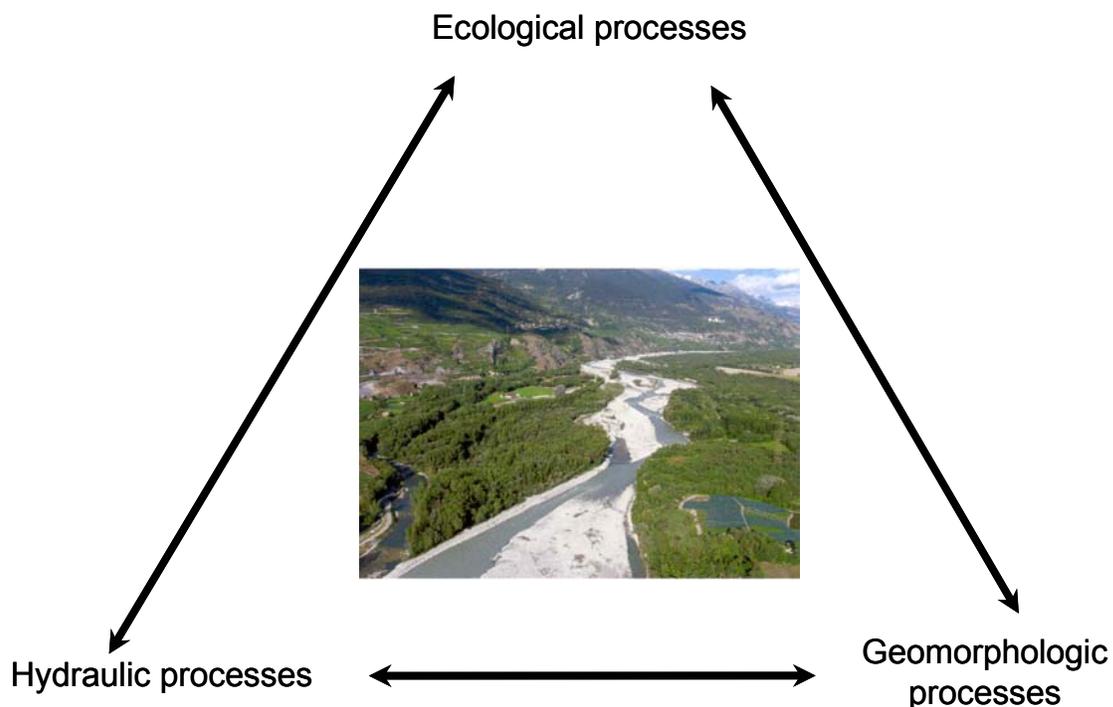
Floodplain dynamics result from the interaction of ecological, hydraulic and geomorphologic processes (River Rhone at Pfynwald, Valais, Switzerland; Photo taken by G. Mathier)

River management consisted historically in channelizing, diking, channel shifting or abandonment of channels. This resulted in an overall simplification of the spatial diversity of the river and the riparian area. During the last decades river management approaches changed dramatically, aiming now to be more multi-functional: safety against flood, water resources utilization, amenity for human life or increase of ecological values are only a selection of such functions. Research and practical experiences made strongly suggest that only the control of an interrelated system of flow, geomorphology and vegetation makes the fulfilment of these functions possible (Tsujimoto, 1999).

## CURRENT RIVER MANAGEMENT – PROBLEMS, OBJECTIVES AND REQUIREMENTS

The problems of current river restoration projects in Central Europe, their general objectives and requirements can be illustrated at the case of the 3$^{rd}$ Rhone Correction Project in Valais (Switzerland).

The River Rhone is termed to be the vertebral column of the Valais, as it dictates in multiple ways the economic and cultural life of the Rhone valley area. With the 1$^{st}$ (starting 1860) and the 2$^{nd}$ (starting 1928) Rhone Correction the prior free flowing river was completely canalized from Brig to the Lake of Geneva, entailing the gain of arable lands but also the loss of highly precious nature values. Actually less than 10 % of the primal riparian area is remaining. However, the flooding events in 1987, 1993 and 2000 in Valais revealed that flood protection is no more assured. Hence, the Canton of Valais initiated in 2000 the 3$^{rd}$ Rhone Correction Project. This new project is conceived to satisfy the principles of sustainability in considering socio-economic, cultural and ecological interests. The general revitalization concept of the River Rhone is based on three axes: more space to increase biological exchange with other habitats, more diversity as the actual riparian area is a monotonous habitat, and more liberty to allow also hydrodynamic processes to occur. One of the possible measures investigated is the enlargement of the section between the levees, where the within levee area will have dynamics mostly driven by hydraulic, geomorphological and ecological processes. Because of the high pressure on land-use in the Rhone valley area, its implementation will further intensify the public debate. That is why the width of the fluvial corridor (*i.e.* the area allocated mainly to flood protection) is an important design parameter. In fact, another important aspect is that the uncertainty of vegetation and landscape development after revitalization,

which often entail negative attitudes of the public towards nature conservation projects. Therefore reliable vegetation succession models are needed not only to provide indications about the ecological consequences of revitalization measures, but also to support and enhance the decision-making process. Stakeholders need to have a scientific basis concerning the relationship between fluvial corridor design and the associated flood protection and ecological benefits. Ecological benefits, in terms of biodiversity, landscape-ecological importance of corridors or in terms of specialized ecological functions, like the maintenance of water quality. At the same time there is a scientific need for a better theoretical understanding of vegetation dynamics in riparian areas and the responsible driving-processes (*e.g.* ecologic, hydraulic). Hence, long-term predictions studies of riparian vegetation dynamics can be very helpful and are even needed in river restoration projects like the one at the River Rhone.

## VEGETATION DYNAMICS MODELLING IN RIPARIAN AREAS

In an attempt to predict the response of riparian vegetation to foreseen changes in flow regime, two major types of analytical models have been developed: (1) realized niche models, which assume that vegetation is in a static-equilibrium with the environmental conditions and therefore utilize statistical relationships between measured environmental variables and species distributions; and (2) process-based models, which consider that vegetation is in transient dynamics including therefore some component of dynamic change of abiotic and biotic conditions (Bolliger *et al.*, 2000; Merritt and Cooper, 2000). To the first type belong the models which relate measurable environmental and physiological constraints on the distribution of plant species, cover types, life-forms, phyto-sociological associations or vegetation zones (*e.g.* Auble *et al.*, 1994; Michiels and Aldinger, 2002). Along morphologically-stable stream channels changes in growing season flow volume, seasonal timing and sequencing of flooding or the frequency and duration of flooding have been incorporated in predictive vegetation models (*e.g.* Stromberg, 1993; Toner and Keddy, 1997). At the landscape level, geographic information systems (GIS) have been used to analyze spatio-temporal land cover evolution of riparian areas to determine landscape-ecological characteristics (*e.g.* diversity of land cover categories, dominance, patch size). For instance, Mendoça-Santos and Claramunt (2001) combined a deductive approach based on quantitative analysis of geographical changes of land-cover categories (*e.g.* water, open forest, non-alluvial forest) with an inductive approach based on qualitative analysis of the spatio-temporal processes (*e.g.* site history) that generate these changes. Nevertheless, the

authors outline that, in view to approach these processes and to explain the causal dimension a methodological framework that includes the analysis of causal links, is still necessary to clarify the relationships between events and changes. Hence, the lack of the so-called realized niche models is that the relationships are based on the assumptions that vegetation is in equilibrium and that the expression of plant response to the environment is limited to reproduce present day conditions. However, the relationships may no more be valid after change of the environmental conditions (*e.g.* increase of nutrient availability), as they can only be applied to the conditions under they have been fitted (Bossel, 1991). Process-based modelling covers this lack by simulating dynamically the main biotic and abiotic processes responsible for vegetation development, as well as the respective vegetation response. They follow the dynamic transient concept in which landscape is considered as a shifting mosaic steady state due to continuous natural and anthropogenic disturbances and successions. In the family of dynamic transient models fall the individual-based gap models (*e.g.* FORSUM; Kräuchi, 1994) or the spatially-explicit distribution-based forest succession models (*e.g.* TreeMig; Lischke *et al.*, 2005). These models have key features that allow a dynamic description of the vegetation pattern: (a) responses of individual plants or plant cohorts to the environment; (b) how these modify their environment; and (c) how accidents of establishment and mortality are amplified through the non-linear processes of plant-environment feedbacks. Based on the parent model JABOWA (Botkin *et al.*, 1972) a wide variety of forest gap models have been developed for specific regional analysis of forest dynamics. The models differ both in the formulation of fundamental processes (growth, regeneration and mortality) as well as in the nature of additional processes or phenomena which they incorporate (Bugmann *et al.*, 1996) according to the different ecosystems they were adapted to. For an overview about the evolution of Gap models, see for example Bugmann *et al.* (1996) and Bugmann (2002). Within the existing forest succession models, only a few tried to simulate riparian forest dynamics in floodplain areas. We can cite the models SWAMP (Phipps, 1979), FORFLO (Pearlstine *et al.*, 1985) and SEEDFLO (Hanson *et al.*, 1990). The latter is based on FORFLO and integrates seed dispersal processes. However, they are not conceived for river systems found in Central Europe (*e.g.* alpine river systems) and do not address explicitly environmental influences like nitrogen scarcity or drought stress important for certain riparian systems, nor they cover integrally the vegetation-hydraulics interaction (*e.g.* mechanical and physiological flooding stress, vegetation roughness).

Complexities of ecological processes in riparian areas require process-oriented and scale-conscious interdisciplinary studies integrating plant ecology and biogeography

with hydrology and geomorphology (Bendix and Hupp, 2000). However, although recognized as important (Malanson, 1993; Richards *et al.*; 2002), a model integrating the dominant driving-processes of riparian areas (*e.g.* ecological processes, hydraulic processes) is not yet available at the desired temporal and spatial scales, even if they would be required for a better theoretical understanding of the riparian system and its functioning. As far as we know, simulations of spatially-explicit riparian forest dynamics for Central European conditions using process-based approaches have never been done so far.

## OBJECTIVES AND OUTLINE

As mentioned, there is an increasing interest (*e.g.* landscape planers, scientists) in developing riparian vegetation dynamic models that consider the dominant driving-processes in riparian areas. The present thesis aims to develop a process-based, spatially-explicit riparian forest dynamics model by integrating, improving and completing driving-processes of existing upland forest succession models, according to the ecological gradients and processes observed in riparian areas. This in view of simulating riparian forest dynamics at different fluvial corridor widening designs, and to provide by this a scientific basis concerning the relationship between design variants and associated ecological values.

More specifically the objectives can be described as follows:

- develop a model to simulate natural riparian forest dynamics for Central European conditions (*i.e.* without silvicultural management interventions) based on the dominant driving-processes of riparian areas;
- provide a better understanding of riparian forest dynamics and its driving-processes; and
- provide a scientific basis about the ecological consequences of restoration measures, particularly for different fluvial corridor widening designs, in order to support and enhance the decision-making processes in river restoration projects.

This thesis consists of five chapters where each of them corresponds to an independent scientific research paper. Based on the modelling gaps cited in the previous section, the first three chapters are closely related and cover the topic of woody vegetation response to flooding. The first of the three reviews the knowledge on the response of Central European tree and shrub species to flooding and

highlights the main biotic and abiotic factors that influence species response. The second suggests a classification of the Central European tree and shrub species into flooding tolerance classes by use of clustering analysis and the third presents a new modelling approach of flooding stress response of tree and shrub species by use of fuzzy logic. Next, the fourth chapter develops a new quasi-mechanistic vertical root growth model for Central European tree and shrub species. A dynamic modelling of forest dynamics requires also a dynamic modelling of vertical root growth. This is needed in the modelling of the resistance of trees and shrubs to drag force, as well as for a better modelling of the soil water balance. Finally, the fifth chapter gives an overview of the new spatially-explicit riparian forest dynamics model RIFOD, its development, evaluation and application at the River Rhone in Valais.

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# Flooding tolerance of trees and shrubs – Case of Central Europe species

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## ABSTRACT

Extensive efforts have been made in recent years to restore rivers with a view to increasing the ecological value of riparian areas and the surrounding landscape and to improving the protection provided against extreme flooding events. One of the important factors for the successful establishment and survival of tree and shrub species in enlarged river corridors (particularly in lowlands) – and in retention basins – is their capacity to survive in anoxic conditions, *i.e.* their flooding tolerance. The importance of improving our understanding of flooding tolerance and the associated factors is underlined by the increasing interest shown in these issues by landscape planners and forestry services throughout Europe. Knowledge about the physiological and metabolic response of most Central European tree and shrub species is still incomplete. From a management perspective there is a high level of interest in exploiting factors that incorporate these physiological and metabolic processes – in ways that are easy to implement and to evaluate in the field. This paper presents a synthesis of knowledge available on the response of Central European tree and shrub species to flooding and highlights the main biotic and abiotic factors that influence species response. The modelling of the impact of flooding on plant species, the success of restoration projects, the planning of retention basins and even the estimation of the economic repercussions of flooding events on forestry could be improved through better knowledge of the flooding stress response of individual tree and shrub species arising from more systematic investigation.

*Keywords: Central Europe, flooding tolerance, processes, anoxia, riparian forest, river restoration*

## INTRODUCTION

Extensive efforts have been made in recent years to restore rivers (and their systems) with a view to increasing the ecological value of riparian areas and the surrounding landscape (creating corridors) and to improving the protection provided against extreme flooding events (Buijse *et al.*, 2002). 'River widening' (*e.g.* Habersack *et al.*, 2000), *i.e.* the enlargement of the section between the levees with the aim of re-establishing quasi-natural river dynamics and the associated typical riparian vegetation, is a popular restoration measure. The ecological success of such restoration projects, and river restoration in general, depends on the information available on the interacting ecological, hydraulic and geomorphological processes responsible for riparian vegetation succession. Apart from life history strategies (*e.g.* seed dispersal strategies, vegetative growth), one of the important factors for the successful establishment and survival of tree and shrub species in enlarged river corridors (particularly in lowlands) – and in retention basins – is their tolerance to flooding (Streng *et al.*, 1989).

In general, flooding tolerance is evaluated (quantified) in terms of the growth response of trees, the level of injury sustained and survival (Kozlowski, 1997) in relation to specific flooding characteristics, mainly flooding depth and duration. The term 'flooding tolerance' occasionally also includes species life history strategies (*e.g.* stem flexibility, high number of seeds) which enable survival in highly disturbed areas, however, in the context of this paper, flooding tolerance is used to express the capacity to survive in anoxic conditions (Hook, 1984). The lack of oxygen affects vital physiological and metabolic pathways and is expressed in symptomatic terms by a decline in growth or even the death of the plant species.

The importance of improving our understanding of flooding tolerance and the associated factors is underlined by the increasing interest shown in these issues by landscape planners and forest services throughout Europe. Important investigations were carried out on the river Rhine in Germany in the aftermath of the extreme flooding events of 1987 and 1999. The aim was to provide a better understanding of the impact of flooding on tree species and to relate flooding depth and duration to the extent of tree damage observed. Based on the findings of these investigations, tolerance thresholds were proposed for each species which have been incorporated into forest management practices along the river Rhine and into the planning of retention basins (Pfarr, 2002). However, conflicting observations revealed that flooding tolerance is more complex than expected and the question remains as to what we really know about the effect of flooding or flooding tolerance of tree and

shrub species, in particular of Central European tree and shrub species. Most of the studies on flooding tolerance were carried out overseas and there exist some excellent reviews that provide important insights into the 'flooding tolerance' mechanisms, including the associated anatomical and physiological adaptations, of mainly non-European tree and shrub species (*e.g.* Hook and Crawford, 1978; Bell and Morley, 1979; Kozlowski, 1984; Armstrong *et al.*, 1994). One of the main ways in which plants adapt to flooding involves the capacity of aerial tissues to absorb $O_2$, basipetal $O_2$ transport through the stems, diffusion of $O_2$ out of roots to oxidize the rhizosphere for the purpose of increasing absorption of macronutrients by roots and the oxidizing of toxic compounds in flooded soils into non-toxic compounds. Morphological adaptations, such as hypertrophied lenticels, aerenchyma tissues and adventitious roots increase the uptake of $O_2$ by aerial tissues and promote its transport into the root system. In addition to the supply of oxygen, the survival of flooding by woody plants depends on the ability to control metabolism, the availability of abundant energy resources, the provision of essential gene products, the synthesis of macromolecules and, finally, protection against post-anoxic injury (Armstrong *et al.*, 1994). These metabolic processes, morphological and physiological adaptations have also been observed in some well-analysed European species, in particular with *Alnus glutinosa* and *Salix alba*. However, the knowledge of the physiological and metabolic response of most of the other Central European tree and shrub species remains incomplete. From a management perspective, there is a high level of interest in exploiting factors that incorporate these physiological and metabolic processes, but in ways that are easy to implement and to evaluate in the field. This is evident in the opportunistic field observations that do not relate tree damage caused by flooding to detailed physiological or morphological processes, but which try to find a relationship to more easily quantified factors (*e.g.* flooding depth, flooding duration). However, the question remains as to the ways in which biotic and abiotic factors affect species response and whether they can actually be used to express flooding tolerance. In order to answer this question in-depth knowledge is required with respect to the nature of these biotic or abiotic factors, the general response of the individual species to these factors and their links to physiologic and metabolic processes.

Opportunistic field observations of adult tree and shrub species in Europe have mainly been carried out on the rivers Rhine (*e.g.* Krause, 1982; Dister, 1983; Späth, 1988; Hügin and Heinrichfreise, 1992; Splunder *et al.*, 1995; Siebel and Bouwma, 1998; Biegelmaier, 2002; Späth, 2002), Elbe (*e.g.* Patz *et al.*, 2000; Roloff *et al.*, 2002), Danube (*e.g.* Karpati and Karpati, 1971), Oder (*e.g.* Gorzelak, 2000) and Rhone (*e.g.* Pautou and Decamps, 1985). More systematic studies of seedlings have

also been carried out under controlled laboratory conditions (*e.g.* Vester, 1972; Hughes *et al.*, 1997; Siebel and Blom, 1998; Siebel *et al.*, 1998). A considerable proportion of the information available on the flooding tolerance of Central European tree and shrub species consists of qualitative data (*e.g.* Siegrist, 1913; Moor 1958; Ehlers, 1960; Goettling, 1968; Heller, 1969; Wendelberger, 1973; Gulder, 1996). However, a synthesis of the field observations and laboratory studies on Central European tree and shrub species with respect to the factors that influence flooding response has not yet be carried out. Thus, in this paper we attempt to summarize the available knowledge about the response of Central European tree and shrub species to flooding and, with the help of the experience gained overseas, to highlight the main biotic and abiotic factors that influence species response to flooding.

We expect to provide helpful insights for future modelling approaches implemented in the context of river restoration projects and possibly also to contribute to the improvement of experimental set-ups for data collection in the field with a view to defining tolerance thresholds.


## SPECIES RESPONSE TO SUBMERSION

Plant responses to submersion vary. They include injury, inhibition of seed germination, vegetative and reproductive growth, changes in plant anatomy, and promotion of early senescence and mortality (Kozlowski, 1997). However, the most significant and common symptom found in trees affected by flooding is a decline in shoot growth (Dickson *et al.*, 1965; Kozlowski, 1984; Frye and Grosse, 1992; Blom *et al.*, 1994; Ewing, 1996; Gravatt and Kirby, 1998). Frye and Grosse (1992) analysed the growth response of tree seedlings of 22 mainly European species following a 120-day flood. The study revealed an extremely high reduction of height grown for *Tilia cordata, Prunus padus, Acer pseudoplatanus, Prunus serotina* and *Acer saccharinum* together with a very poor recovery in the second year for the species *Rhamnus cathartica, Sorbus aucuparia, Betula pubescens, Betula pendula* and *Acer campestre*. An increase in diameter growth was observed for *Quercus robur* and *Fraxinus excelsior*. This phenomenon was often observed in flood-tolerant species as they produce more intercellular spaces and lower density cells, thus enabling oxygen transport.

Soil inundation reduces not only the shoot growth, but also the root growth of most woody plants. The lack of oxygen, the accumulation of toxic metabolites (*e.g.* aldehydes, organic acid, ethanol) and the accumulation of carbon dioxide due to the restriction of the soil-atmosphere gas exchange by the flooding (Ponnamperuma,

1984) can inhibit root formation and branching and the growth of existing roots and mycorrhizae as well as causing root decay (Kozlowski, 1997). Hence the reduction of shoot and root growth is the result of the inhibition or disruption of vital physiological and metabolic processes or pathways. A reduction in oxygen availability in the rhizosphere reduces not only the absorption of oxygen, but also water and macronutrient uptake (*e.g.* nitrogen, phosphorus, potassium) by the root system. It has been shown that waterlogged conditions cause a decline in nitrogen fixation because oxygen, which is necessary for nitrogenase activity, becomes a limiting factor. This phenomenon was observed in *Alnus incana* seedlings (Hughes *et al.*, 1997) which, after waterlogging for more than approximately seven consecutive days, promoted little growth and displayed rapid deterioration in plant health. According to Ewing (1996), plants respond to flooding with decreased photosynthesis, which in some cases is associated with decreased stomatal conductance resulting in a diminution of productivity (accumulation of carbon) and leaf expansion. The metabolism is affected by the lowering of the concentration of ATP due to the blocking of oxidative phosphorylation. Flooding not only reduces the rate of photosynthesis, but also the rate of translocation of photosynthetic products from sources (*e.g.* leaves) to various sinks (*e.g.* roots); see Gravatt and Kirby (1998). Flood-induced reduction of photosynthesis was also recorded for *Betula pendula, Fagus sylvatica, Malus domestica, Populus* spp., *Prunus* spp., *Quercus petraea, Quercus robur* and *Tilia cordata* (Kozlowski, 1997).

Due to the inhibition of root growth in anoxic conditions, shallow spreading root systems are characteristic of sites with high water tables as observed in many riparian areas in Europe (Köstler *et al.,* 1968; Mitscherlich, 1971; Lehnardt and Brechtel, 1980; Hainard *et al.*, 1987; Polomski and Kuhn, 1998). With the exception of *Quercus robur, Pinus sylvestris* and *Alnus glutinosa*, which were observed to have entered the groundwater zone (Lehnardt and Brechtel, 1980), in conditions involving a permanently high groundwater level even deep-rooting species develop a shallow root system. In soils with an increased groundwater influence, such as Pseudogley or Gleye soils, rooting depths do not vary significantly between tree species (Lehnardt and Brechtel, 1980). Thus root growth is typically reduced to a higher level than stem growth which explains the decreased root/shoot ratio in riparian areas (Kozlowski, 1997). Soil inundation also has profound effects on seed germination as the activation of the physiological processes necessary for seed germination requires the supply of $O_2$ which is severely reduced by soil inundation. Hence the seed germination of many species is prevented or postponed (Kozlowski and Pallardy, 1997).

# THE FACTORS THAT INFLUENCE FLOODING TOLERANCE

The differences in species response to flooding can be explained mainly by their genetic constitution, *i.e.* their ability to react to the resulting stress in morphological, physiological and metabolic terms. However, all species, *i.e.* both well-adapted and non-adapted species, present response patterns that are influenced by other abiotic features such as the 'timing', 'depth' and 'duration' of flooding and biotic factors such as 'development stage' and the aforementioned 'genetic constitution'. We have synthesized the main abiotic factors that affect flooding tolerance and their relation to the plant metabolism in the form of a conceptual model (see Figure 1). However, final flooding stress response depends on the biotic factors of each species. The conceptual model is discussed in the following sections. More detailed information on the metabolic response of plants to flooding can be found in Armstrong *et al.* (1994) and Crawford (1989).
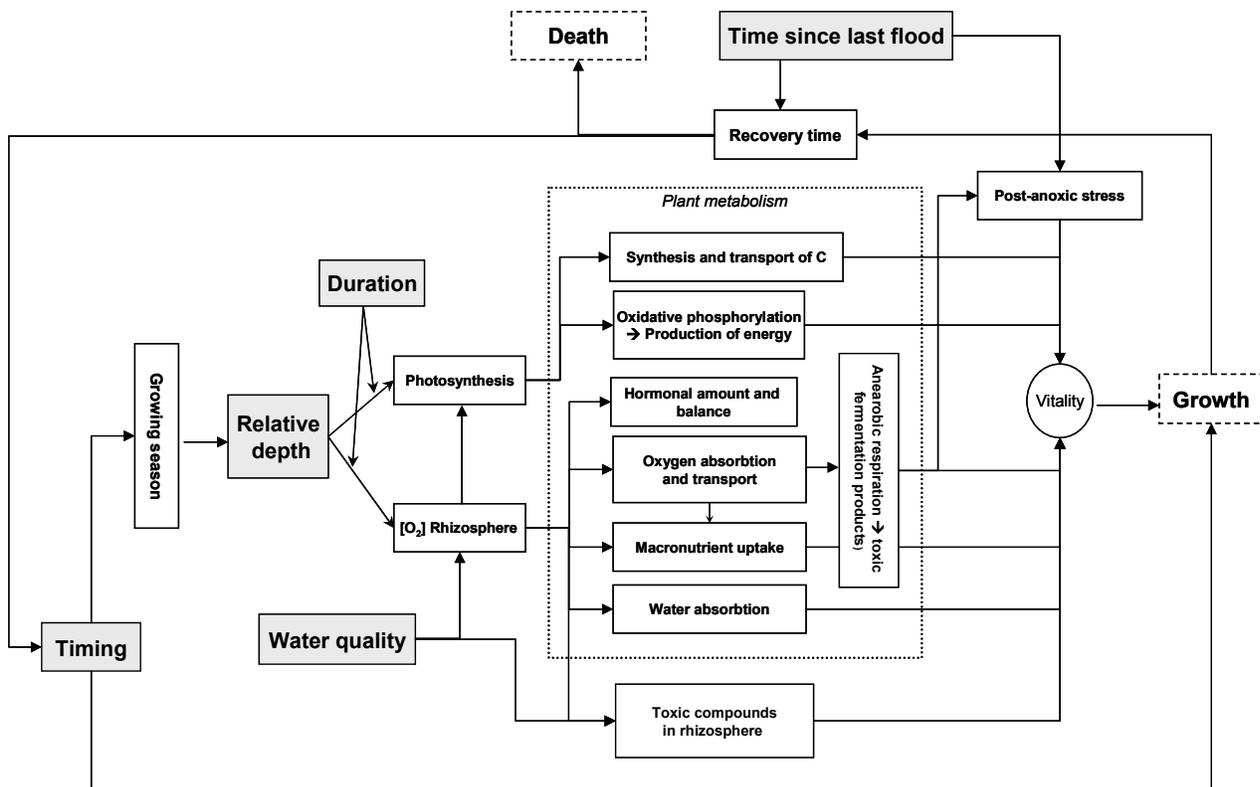


Figure 1: Conceptual model illustrating the main abiotic factors affecting flooding tolerance and their relation to the plant metabolism of tree and shrub species.

## A. BIOTIC FACTORS

## A.1 Genetic constitution

Most of the adaptations to flooding described in the literature were morphological in nature, *e.g.* development of lenticels and adventitious roots. Table 1 provides an overview of the main anatomical and morphological adaptations found in Central European tree and shrub species.

*Lenticels*

Hypertrophied lenticels develop around the stem, generally where a stomate once occurred. They become a pathway through which gases, in particular $O_2$, can diffuse to the living cells of the bark. In addition, as observed for *Salix alba* (Hook and Scholtens, 1978), potentially toxic compounds associated with anaerobiosis (including acetaldehyde, ethanol, and ethylene) are released through the lenticels. Hook and Scholtens (1978) pointed out that although lenticels on the seedlings of several woody plant species are known to provide access for $O_2$ there is still a lack of quantitative data on the permeability of bark in mature trees. However, the blocking of lenticels at the bases of *Salix* spp. cuttings severely inhibited $O_2$ diffusion from the roots to an anaerobic medium, hence preventing oxidation of the rhizosphere (Hook, 1984). As early as 1912, Siegrist (1913) reported the development of lenticels enabling the survival of low flooding at the stem base of *Salix* spp*.* and *Populus* spp. in his study of the river Aare in Switzerland. However, Tubeuf (1912) also assumed that during flooding the oxygen transport through the lenticels at the stem base is limited or completely halted, thus the respiration-active cambium dies. Hence, Tubeuf claimed that species with a smooth bark (*e.g. Fagus sylvatica, Acer* spp*., Fraxinus excelsior*) are more sensitive to the effects of flooding than species with a coarse bark (*e.g. Salix* spp., *Populus* spp., *Ulmus* spp., *Quercus* spp*.),* as a rough bark makes it possible to retain oxygen for a longer period. The importance of the lenticels is also highlighted by Gorzelak (2000) who claims that the absolute submersion depth of trees is not important if the stem base, including lenticels, is inundated. Frye and Grosse (1992) identified *Alnus glutinosa, Alnus incana, Betula pubescens* and *Populus tremula* as avoiding anaerobic stress due to the improvement of oxygen transport to the roots by pressurized gas transport. This physical adaptation of trees to anoxia is based on the thermo-osmotically active partition localized in the phellogen layer of the lenticels. Development of lenticels has also been reported for other Central European tree and shrub species; see Table 1.

Table 1: Overview of anatomical and morphological adaptations to flooding of Central European tree and shrub species.

| Species | Adventitous roots | Lenticels | Aerenchyma |
|---|---|---|---|
| *Abies alba* | ✔ a | | |
| *Acer campestre* | ✔ a,b,d | ✔ b | |
| *Alnus glutinosa* | ✔ a,b,c,d | ✔ a,b,g | ✔ f,g |
| *Alnus incana* | ✔ a | ✔ g | |
| *Alnus viridis* | ✔ a | | |
| *Amelanchier ovalis* | ✔ a | | |
| *Betula pendula* | | ✔ a | |
| *Cornus sanguinea* | ✔ a | | |
| *Corylus avellana* | ✔ a | | |
| *Frangula alnus* | ✔ a | | |
| *Fraxinus excelsior* | ✔ b,c,d | ✔ a,b | ✔ g |
| *Hippophae rhamnoides* | ✔ a | | |
| *Ligustrum vulgare* | ✔ a | | |
| *Lonicera xylosteum* | ✔ a | | |
| *Picea abies* | ✔ a | | |
| *Pinus sylvestris* | | ✔ d | ✔ h |
| *Populus spp.* | | ✔ c | |
| *Populus alba* | | | ✔ h |
| *Populus nigra* | ✔ b,d | ✔ b,c | |
| *Populus tremula* | | ✔ g | |
| *Prunus avium* | ✔ a | | |
| *Prunus domestica* | | | |
| *Prunus padus* | ✔ a | | |
| *Prunus spinosa* | ✔ a | | |
| *Pyrus communis* | | ✔ d | |
| *Quercus robur* | ✔ b,d,k | ✔ b | |
| *Rhamnus cathartica* | ✔ a | | |
| *Salix spp.* | | ✔ c | |
| *Salix alba* | ✔ d,l | ✔ i,j | |
| *Salix appendiculata* | ✔ a | | |
| *Salix caprea* | ✔ l | | |
| *Salix cinerea* | ✔ a,i,l | | |
| *Salix fragilis* | ✔ a,d,l | ✔ l | ✔ l |
| *Salix m. nigricans* | ✔ l | ✔ l | ✔ l |
| *Salix pentandra* | ✔ a,l | ✔ l | ✔ l |
| *Salix purpurea* | ✔ a | | |
| *Sambucus nigra* | ✔ a | | |
| *Sorbus aucuparia* | | | |
| *Tilia cordata* | ✔ a | | |
| *Ulmus glabra* | ✔ a | | |
| *Ulmus minor* | ✔ b | ✔ b | |
| *Viburnum opulus* | ✔ a | | |

(a) Polomski and Kuhn (1998), (b) Siebel *et al.* (1998), (c) Siegrist (1913), (d) Kozlowski (1997), (e) Köstler (1968); (f) Yamamoto *et al.* (1995), (g) Frye and Grosse (1992), (h) Armstrong and Read (1972), (i) Hook (1984), (j) Hook and Scholtens (1978), (k) Schmull and Thomas (2000), (l) Gill (1970)

*Aerenchyma*

Aerenchyma tissues are extensive intercellular air spaces that form continuous passageways allowing the diffusion of oxygen from the aerial portions of the plants to the roots. They are usually formed by the separation or disintegration of the cortical cells leaving spoke-like strands of living cells behind that extend from the outer cortex to the endodermis. Their formation is triggered by the presence of ethylene which stimulates cellulose activity and promotes the disintegration of cortex cells. According to Polomski and Kuhn (1998), this can be seen as an adaptation to anoxic conditions. They point out that most flood-tolerant species are more inclined to develop aerenchyma in the roots than the shoots and that species not responding directly to soil anaerobiosis by enlarging their internal air spaces, typically undergo anoxia in their roots. Aerenchyma tissues were observed in *Alnus glutinosa* (Köstler *et al.*, 1968), *Fraxinus excelsior* (Frye and Grosse, 1992), *Salix fragilis, Salix myrsinifolia nigricans* and *Salix pentandra* (Gill, 1970)*.*

*Adventitious roots*

After death of the original roots due to flooding, adventitious roots are produced on the original root system and on the submerged portions of stems. These flood-induced roots grow generally negatively geotrop and are usually thicker and have larger intercellular spaces than roots growing in well-aerated soils. Furthermore, they are better adapted to anoxic conditions as they can tolerate higher $CO_2$ concentrations or are able to maintain respiration, despite the lack of oxygen. Adventitious roots also increase water absorption by the roots, they oxidize the rhizosphere and transform some soil-borne toxins into less harmful compounds and, finally, they increase the supply of root-synthesized gibberellins and cytokinins to the leaves (Kozlowski, 1997). According to Polomski and Kuhn (1998), the development of adventitious roots is stimulated by the increase of ethylene concentration in the shoot parts of the trees or due to an external increase of the compound in the soil solution. Furthermore, the dieback of the older roots may favour the development of younger roots, as observed for *Salix* spp., *Populus* spp. and *Alnus* spp. A lot of adventitious roots also contain aerenchyma cells which rapidly take over the oxygen supply, as observed for *Salix pentandra, Salix nigricans* and *Salix fragilis* (Gill, 1970). Schmull and Thomas (2000) analysed the morphological and physiological reactions of one-year-old *Quercus robur, Quercus petraea and Fagus sylvatica* seedlings to waterlogging. In contrast to *Fagus sylvatica*, the Quercus species, in particular *Quercus robur*, was able to develop roots – even within the waterlogged horizon – and to form adventitious roots. In his study on the river Aare in Switzerland, Siegrist (1913) observed the development of adventitious roots at the stem base of *Salix*

spp., *Populus* spp., *Alnus glutinosa* and *Fraxinus excelsior*. The development of adventitious roots has also been reported for other Central European tree and shrub species; see Table 1. Hypertrophied lenticels, aerenchyma tissues, and adventitious roots may be present in the same plant (Hook, 1984) as is the case, for example, with *Alnus glutinosa, Fraxinus excelsior, Salix pentandra, Salix nigricans* and *Salix fragilis.*

*Metabolic adaptations*

In the experiments carried out by Vester (1972) the glycerol content (non-toxic end product) increased rapidly in *Alnus incana* roots during the first few days of flooding. This production of glycerol could continue unhampered in the absence of oxygen and provides an alternative to ethanol as the end product of anaerobic respiration. Similar mechanism have been observed for *Salix cinerea* which by decreasing root aeration, increased root contents of non-toxic pyruvate, malate and succinate, by by-passing the oxidative conversion through the Krebs-cycle and avoiding therefore the production of ethanol. Siebel *et al.* (1998) suggested that the tolerance of *Populus nigra* was mainly due to physiological or metabolic adaptations; as was the case with *Populus nigra* – a tolerant softwood species – little morphological response could be identified after complete flooding.

## A.2 Development stage

Most authors (*e.g.* Gill, 1970; Hall and Smith, 1955; Kozlowski, 1997; Siebel and Blom, 1998) agree that adult trees tolerate flooding better than overmature trees or seedlings of the same species. Thus, even those species rated as flood-tolerant may be quite sensitive at the seedling stage. However, little is still known about the changes in the sensitivity of tree seedlings to total submergence during their early years (Siebel and Blom, 1998). However, Siebel and Blom (1998) managed to show that the relative decrease in biomass caused by flood damage was slower in three-year-old seedlings than in one-year-old seedlings, thus the older seedlings survived total submergence longer than young seedlings. *Alnus glutinosa* seedlings were small when flooded in their first season and had therefore a lower tolerance, however as they grew rapidly, older seedlings were more tolerant than *Fraxinus excelsior*. *Populus nigra* seedlings displayed the highest tolerance in the second year. Popescu and Necsulescu (1967) observed that 1-4.5 year-old *Populus nigra* trees suffered a much higher level of injury than those that were at least five years old.

According to Siebel and Blom (1998), rapid youth growth and the capacity to avoid total submergence are not the only factors that enable some species to develop successfully on floodplains and that there could be a difference in tolerance based on the age of a species and the capacity to develop physiological or metabolic adaptations more easily. The authors suggest that the lower tolerance of *Alnus glutinosa* in the first year as compared with *Quercus robur* and *Fraxinus excelsior* may also relate to the higher levels of reserves in the cotyledons, as they have larger seeds. This argument is also mentioned by Streng *et al.* (1989). However, based on the experimental flooding of *Pinus sylvestris* and *Larix europea* in different age classes, Vester (1972) claims an inverse relationship between plant age and size and flooding tolerance. In the case of flood-intolerant species, damage increased with the age and size of the seedlings, whereas the ability to resist damage appeared to be independent of age and size in the flood-tolerant species. Thus, as argued by Siebel and Blom (1998), the flooding tolerance of seedlings, compared to adults, needs further investigation.

## B. ABIOTIC FACTORS

## B.1 Flooding depth

Most authors accept that the depth of water influences flooding tolerance and thus confirm the importance of making a distinction between complete inundation, partial inundation and soil saturation (Gill, 1970; Hall and Smith, 1955; Bratkovich *et al.*, 1993; Siebel *et al.*, 1998).
In general, injury increases as soil saturation progresses, first to partial inundation and then to complete inundation. A species that can survive a certain period of soil saturation or partial inundation will often fail to survive the same period of complete inundation (Gill, 1970). Even in species with a similar water tolerance, taller plants probably have a greater chance of survival than shorter ones, particularly in conditions of relatively deep flooding (Hall and Smith, 1955). However, once water covers the soil, the depth may have little significance until the lower foliage is covered (Bratkovich *et al.*, 1993; Coder, 1994). At this point tree injury increases in proportion to the percentage of the crown covered by water. Stanturf and Gardiner (2000) highlight the importance of taking relative flooding depth into account, pointing out that even the few species that can withstand extended soil saturation and root anoxia cannot tolerate the submersion of all their leaves, thus tolerance to complete submersion is much lower than tolerance to shallower depths of water. However, Siebel and Blom (1998) suggest that tolerance of total submergence may also

depend on the previous occurrence of non-lethal flooding periods. It can be supposed that the reason of the increasing flooding stress from soil submersion to complete submersion is partially due to a reduction of the ability to transport internally (*e.g.* aerenchyma) and externally (*e.g.* lenticels) oxygen to the roots and out of the roots, affecting consequently plant metabolism; see Figure 1. Moreover, the increased mortality with crown submergence is additionally related to the oxygen deficiency of the submerged aerial tissue during the respiration phase and the reduction of photosynthesis giving rise to the reduction of carbon accumulation and the decline in metabolism by blocking the oxidative phosphorylation. Unlike herbaceous plants, in which $O_2$ enters largely through the leaves, Kozlowski (1997) argues that due to the resistance to gas movement and consumption of $O_2$ by respiration during its movement down the stem, it is unlikely that roots of trees that are beyond the seedling stage are supplied with $O_2$ via the leaves.

The influence of flooding depth on species tolerance was also observed for various Central European species. *Alnus glutinosa* does not tolerate submersion of the entire stem including the lenticels. It is highly sensitive and dies after just a few weeks of complete submersion (Utschig *et al.*, 2001); *Fraxinus excelsior* is similar (Tubeuf, 1912). Marigo *et al.*, (2000) observed that like other riparian hardwood trees, such as *Ulmus minor* and *Quercus robur*, *Fraxinus excelsior* seedlings display a high level of high tolerance to partial submersion, due in part to morphogenetic adaptations (*e.g.* adventitious roots). Nevertheless, because they have relatively slow extension growth rates as compared to softwood trees, they are far more sensitive to total submersion. According to Siebel *et al.* (1998), tolerance of total submergence correlates with tree zonation along the river Rhine, as seedlings of tree species from hardwood floodplain forests, such as like *Fraxinus excelsior, Quercus robur* and *Ulmus minor,* were less tolerant than seedlings of species from softwood floodplain forests, like *Alnus glutinosa* and *Populus nigra*. Once seedlings were totally submerged, the depth of water had no additional effect on their survival. A period of four weeks of total submergence in spring was enough to damage tree seedlings and to reduce their extension growth, whereas partial submergence for up to three months had little or no effect on the extension growth of *Fraxinus excelsior, Quercus robur, Ulmus minor*, *Alnus glutinosa* and *Populus nigra* seedlings. Thus, typical riparian hardwood species also demonstrated a strong morphological response to partial submergence, which explains their tolerance in these flooding conditions.

Apart from the numerous punctual observations, more systematic field studies of species response to flooding were carried out on the river Rhine in Germany after the severe flooding events of the summers of 1987 and 1999. Späth (1988) identified

'vital ranges' and 'critical ranges' of flooding depths for several Central European tree species after the summer flooding in 1987 of the Rhine floodplain in Baden, Germany. In contrast to the vital range, the critical range indicates flooding depths for which tree deaths were also recorded. The most tolerant species were *Salix alba*, with a vital range up to 3.50 m, *Cornus sanguinea* and *Ulmus minor* at 2.40 m and *Alnus incana* at 2.20 m, while the least tolerant species were *Viburnum lantana* at 0.40 m and *Fagus sylvatica* at 0.50 m. Data on flooding depths in relation to the percentage of damaged and death trees can also be found in Biegelmaier (2002), who examined the effects of the relatively short flooding duration (four to six days) of the alluvial forest of the Upper Rhine in Gemark Sasbach-Jectingen in Germany in 1999. According to Biegelmaier (2002), the analysis of the consequences of this flood for the trees prompted the conclusion that flooding depth is more important than flooding duration. Unfortunately, in these studies, as well as in others, no indications are provided on the submersion depth relative to tree height which has previously been shown to be of greater significance than absolute flooding depths. Moreover, the data presented by Biegelmaier (2002), Späth (1988), Krause (1982), and Dister (1983) (all relating to the river Rhine in Germany) can not be directly compared as the measurement conditions (season) differed (Ritterbach, 1991). Moreover, it is not clear whether the data represents extreme tolerated depths or mean values.

Apart from the hydraulic regime of a river, the geomorphology may also affect species' oxygen supply as tree and shrub species can become buried in sediment. This process is particularly important in upland rivers with a high level of geomorphological activity. Schiechtl (1992) comments that, with the exception of *Pinus sylvestris*, the *Salix* species are again the most resistant tree species with respect to burial. *Salix eleagnos* and *Salix purpurea* tolerated burial by sediment to a height of 3.40 m (= 27.0 % of tree height) and 2.20 m (= 29.4 % of tree height) respectively. Schiechtl (1992) also points out that tolerance to burial appears to be strongly dependent on sediment composition. According to Ellenberg (1996), *Salix daphnoides, Salix purpurea* and *Salix eleagnos* are resistant to strong water flow and burial.

## B.2 Flooding duration

Generally, the longer trees are exposed to flooding, the greater the potential for injury. Most trees can tolerate short periods of flooding during the growing season. However, if flooding is recurrent and keeps the soil saturated, injuries will accumulate and serious damage may occur as the decrease in the oxygen supply increasingly affects the trees' biochemical response. Overall, duration of flooding accentuates the effects due to flooding depth; see Figure 1. Hall and Smith (1955) studied the effects of flooding on woody plants in the Kentucky Reservoir (Alabama, US). The study showed that in order to survive indefinitely even the most flood-tolerant species needed to be unflooded for at least 55-60 % of the growing season. According to Gill (1970), year-round root inundation can be tolerated if it is an occasional, isolated event. However, when a habitat becomes flooded for more than 40 % of the growing season, woody species can not colonize it, although it is possible that once established they may survive. Toner and Keddy (1997) come to a similar conclusion in their Canadian study which established a range of 36-38 % of the growing season as representing a barrier to seedling establishment, but less of a barrier to adult tree survival. These observations are only partly confirmed in the European studies. Frye and Grosse (1992) analysed the flooding tolerance of 22 tree species (one-year-old) and observed that the species tolerate a duration exceeding the 40 % limit cited by many authors. Gorzelak (2000) analysed tree damage arising from the flooding of the river Oder in Poland in 1997. All of the *Fagus sylvatica* located in sites that were flooded for longer than four weeks (measured in 1998) died, *Carpinus betulus* suffered severe damage in sites with stagnant water (reduced oxygen content), whereas, similar to the response of *Fraxinus excelsior,* few species located in sites with flowing water suffered damage. All of the *Acer pseudoplatanus* trees died outright, particularly in locations in which the water was stagnant for a short period of time. *Alnus glutinosa* also died under stagnant conditions, but presented nearly no damage under flowing water conditions. *Prunus padus* recovered well in the second year. *Larix decidua* and *Picea abies* died outright, especially under stagnant conditions, but *Pinus sylvestris* survived and presented almost no signs of damage under flowing-water conditions. All of the *Salix* spp. and *Populus* spp. presented no signs of damage, but *Juniperus communis* died. Similarly, Dister (1985) claims that *Fagus sylvatica, Acer pseudoplatanus* and *Acer platanoides* are not typical riparian species as they tolerate only several days of flooding. In his study of the Tide-Auenwald alluvial riparian forest in Germany, Schiechtl (1992) observed that all European Salix species survived flooding for several days without any damage and that within these species, *Salix alba* and *Salix fragilis* appeared to be most resistant and *Salix caprea* the least. Most of the investigations on the response of individual

species to flooding duration (days/growing season) have been carried out in Germany (Krause, 1982; Dister, 1983; Späth, 1988; Hügin and Heinrichfreise, 1992; Späth, 2002; Biegelmeier, 2002). As was the case with the factor 'flooding depth', the data for flooding duration barely allows comparison as the conditions of measurement differed. Nevertheless, in Figure 2 the measurements recorded in 1987 by Späth (1988) at Iffezheim, Upper Rhine, Germany are compared to those recorded after the flooding in 1999 (340 measurement sites between Basle and Mannheim, Upper Rhine, Germany; see Späth, 2002). The measurements were taken during the growing season (1.4 – 30.9). As was the case with flooding depth, the vital range of duration corresponds to periods in which no dead trees were recorded, whereas the critical range of duration corresponds to the point at which the first dead trees were recorded.

Figure 2 reveals that the tolerated flooding durations differ for some species which indicates the involvement of other factors and processes responsible for the flooding tolerance response. Compared to the tolerance threshold of a 40-45 % flooded growing season observed by Hall and Smith (1955), we have established that nearly all softwood species tolerate higher flooding durations.

**Flooding duration in relation to tree vitality (Upper Rhine, Germany)
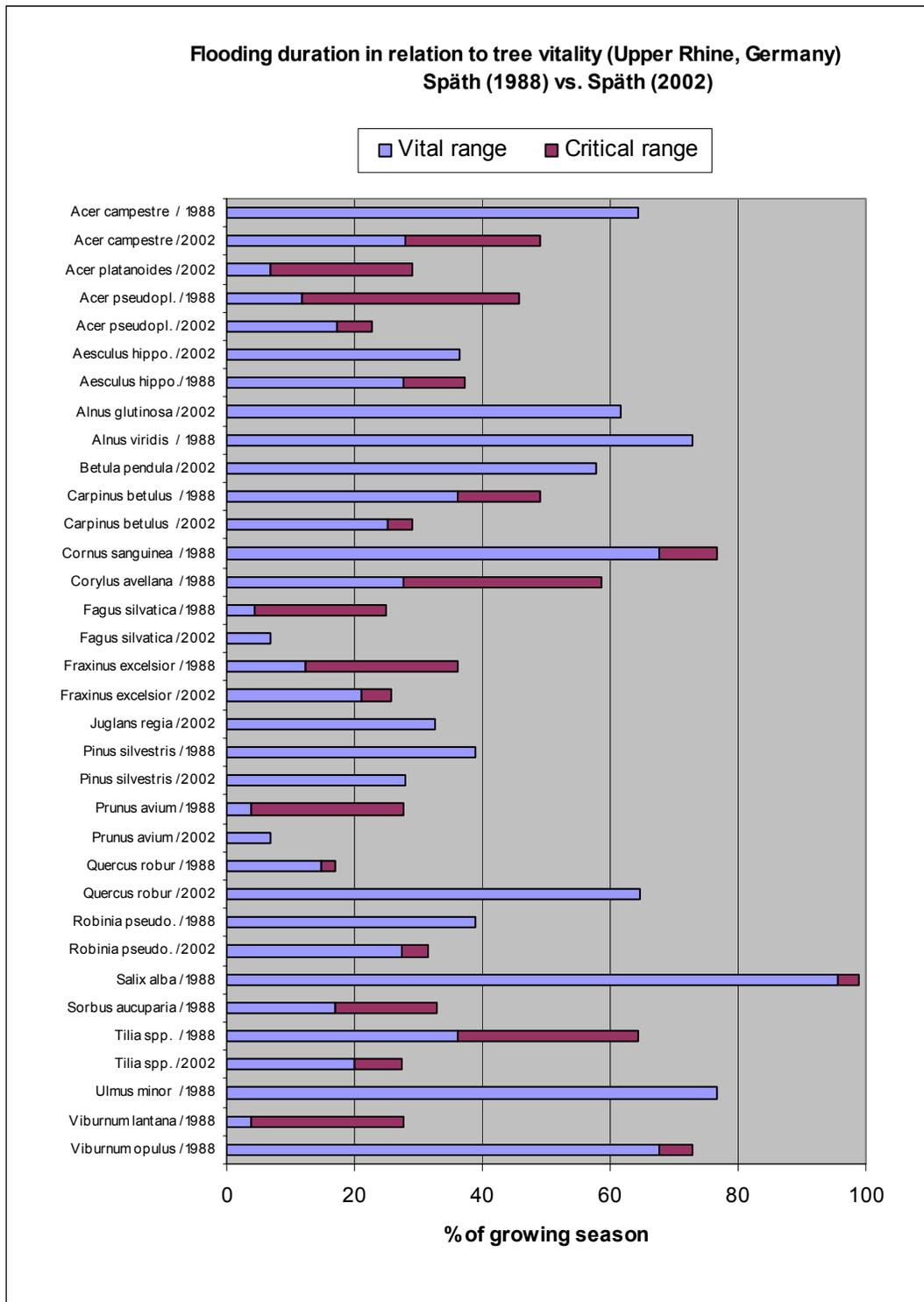Späth (1988) vs. Späth (2002)**

Figure 2: Flooding duration (% of growing season) in relation to tree vitality
(Späth, 1998, 2002; Upper Rhine, Germany).

Pott (2000) measured a flooding tolerance for the hardwood species *Quercus robur* of 96 days/year and 119 days/year for *Ulmus leavis* at a potential retention basin in Lenzen-Wustrow (river Elbe, Germany). The softwood species *Salix viminalis* and *Salix rubra* reached a flooding tolerance up to 165 days/year and 238 days/year (measured only for adult species). The data recorded by Patz *et al.* (2000) on the river Elbe supported Pott's (2000) observation that the limit for softwood species lies at an annual flooding duration 150 days and at 50 days for hardwood species. However, it is not clear how many days of flooding fall within the growing season. Such classifications are often the basis of simplified representations, in which flooding characteristics are not related to the presence of individual tree species, but associated with typical vegetation types or zones, *e.g.* softwood or hardwood zone (Gerken, 1988; Ellenberg, 1996). These classifications can be a helpful tool in terms of the site classification of forests, as has been carried out for the riparian forest of the Rhine. Michiels and Aldinger (2002) provide a recent classification for the Upper Rhine which indicates the alluvial vegetation zonation (low softwood zone, transition soft-hardwood zone, low hardwood zone, medium hardwood zone and high hardwood zone) and the maximum and mean flooding durations for the Upper Rhine between Iffezheim and Karlsruhe, Germany. Although such classifications can be a useful tool in the context of planning processes, they must be considered as spatially-specific and, therefore, of limited relevance as they do not incorporate variations in site conditions, hydrological parameters and ecological requirements. Moreover, they do not address the tolerance limits of individual tree species.

## B.3 Flooding timing

Almost all authors agree that flooding is more harmful if it occurs during the growing season than if it occurs during the dormant season (Hall and Smith, 1955; Hosner and Boyce, 1962; Gill, 1970; Siebel and Blom, 1998; Gorzelak, 2000). Irrespective of its duration, flooding has little or no effect in the dormant season because of the minimal demand for oxygen by roots and micro-organisms in winter. As opposed to this, plant responses to flooding during the growing season include injury, inhibition of seed germination, vegetative growth, changes in plant anatomy and promotion of early senescence and mortality (Kozlowski, 1997). Trees are most vulnerable to the effects of flooding in late spring, just after the first flush of growth. According to Streng *et al.* (1989), early germinating species are at a particular disadvantage if flooding occurs in early spring as the flooding affects them just after germination, whereas late-germinating species can avoid such effects in their first season. Siebel and Blom (1998) succeeded in demonstrating that the timing of flooding within the

growing season had a different effect on the seedling development of *Alnus glutinosa, Populus nigra, Fraxinus excelsior, Quercus robur* and *Ulmus minor*. Severe root mortality and seedling death occurred more rapidly during summer flooding than during spring flooding, even if species had a higher biomass before the summer flooding. Siebel and Blom claim that the total submergence of seedlings in late spring and summer has an important effect on tree zonation in floodplain forest along the river Rhine in Germany.

## B. 4 Flooding frequency / Time since last flood

According to Pollock (1998), the frequency and strength of floods are probably the most important determinant of species diversity within riparian corridors. This corroborates the study carried out by Bedinger (1971) which identified a clear relationship between the distribution of forest species in the Lower White River floodplain (US) and the frequency and duration of flooding. However, according to Hupp and Osterkamp (1996), the bottomland vegetation distributions along the Passage Creek (Virginia, US) was at least partially controlled by inundation frequency and the susceptibility of plants to damage by destructive floods. Palik *et al.* (1999) show that longleaf pine (*Pinus palustris*) survived a 100-year flooding event, even they were believed to have a high mortality when submerged. Thus, the absence of *Pinus palustris* on floodplains can only be due to an intolerance to frequent flooding (Goebel *et al.* 1996).

European studies also exist which highlight the importance of flooding frequency. Siebel and Blom (1998) emphasize the importance of the frequency and timing of flooding. The authors suggest that hardwood floodplain tree species are more adapted to regular but moderate levels of stress induced by total submergence, whereas the softwood tree species are more adapted to irregular and severe floods. They explain this on the basis of the limited ability of hardwood forest trees to become established in the Rhine riparian system due to the current irregular occurrence of high floods in late spring and summer. Similarly, Carbiener and Schnitzler (1990) comment that the spatial pattern of the major flood plain forest communities along in the Rift valley (France/Germany) on the Rhine does not depend on topography, but on temporal processes based on the energy load of flooding and the frequency and periodicity of great floods.

According to Dister (1983), the main problem is the frequency of recurring flooding as the damaged trees are unable to recover. The same argument is also presented by Hughes (1997), who suggests that the influence of a flood event is determined not

only by its magnitude, but also by its position in a sequence of flood events. Depending on the growth pattern of some trees, flood damage effects may be present for two to three years into the future (Coder, 1994), and therefore recovery time required may exceed the time between floods, resulting in an additional weakening of these trees. It can be supposed that the flooding tolerance of trees that are subject to regular floods over several years or in the course of one and the same year decreases because the time needed to re-establish the functioning of biochemical processes and to regain vitality increases and exposure to post-anoxic stress is accentuated. The accumulation of toxic fermentation products and the lack of the enzyme superoxide dismutase (SOD) make plants susceptible to post-anoxic injury when plant tissues are not protected against oxygen damage on return on air (Fry and Grosse, 1992). *Alnus glutinosa* is known to accumulate SOD in its root tissues during soil inundation in order to survive long-term flooding.

## B.5 Flood water quality

Due to the capacity of cold water to hold more dissolved oxygen, cold water is less damaging than warm water (Bratkovich *et al.*, 1993). Similarly, rapidly flowing water is less harmful than stagnant water (Frye and Grosse, 1992) as rapidly flowing water has a higher oxygen concentration due to the permanent mixture of deep and high water layers. This phenomenon has also been observed for adult trees on the river Rhine (Späth, 2002) and the river Oder (Gorzelak, 2000). Flooding tolerance is not only influenced by the oxygen concentration in the water, it is also influenced by the concentration of other chemical compounds which can interfere with biochemical pathways. Floods in agricultural areas can carry various chemicals that have been picked up as runoff from fields and other areas and even from sewage released when treatment facilities become unable to handle large volumes of water. The impact on the vitality of trees and, therefore, also on their flooding tolerance, depends on the type and dosage of the chemicals they were exposed to and on duration of exposure.

## C. EXAMPLE OF FLOODING TOLERANCE CLASSIFICATION

Relative rankings of flooding tolerance of tree and shrub species were indirectly done by describing processes in the field, by analyzing results of experiments under controlled field conditions with seedlings or by evaluating tree damages after large flooding events. The existing flooding tolerance classifications relate or do not relate

each tolerance class to a tolerance range of the specific stress the classification was initially based on (Glenz *et al*., 2005; Chapter 3). As seen in this paper, for many Central European tree and shrub species detailed quantitative knowledge about their flooding stress response in relation to the responsible abiotic and biotic factors is still missing or sparse. Moreover, most of the existing investigations did not consider the same relevant factors at similar plant development stages, which may explain some differences in flooding stress response within a same species. Hence, a systematic classification of a larger set of species into flooding tolerance classes based on their flooding stress response in relation to the highlighted abiotic factors can not be done properly. Glenz *et al.* (2005; Chapter 3) performed a 5 scale tolerance classification of 65 Central European tree and shrub species based on cluster analysis and expert knowledge – considering also the available qualitative and quantitative data; see Table 2. The cluster analysis is based on proxy-data of flooding tolerance consisting of soil moisture preference of the species, light preference, height to the mean water level, as well as the ability to develop morphological and anatomical adaptations to flooding. Being aware of the complexity of flooding stress response (interaction of several abiotic and biotic factors) the authors tried to characterize the different tolerance classes. For example in tolerance class 1 (very low tolerant), only hardwood species presenting nearly no morphological and physiological adaptations to flooding can be found. They tolerate soil submersion, less partial submersion but not complete submersion. Moreover, species of this tolerance class tolerate only short floods and are found on sites of the top hardwood zone of the river Rhine with flooding durations of 5-20 % of the growing season. On the other hand in class 5 (very high tolerant), softwood species developing morphological and physiological adaptations to flooding were grouped, tolerating long floods, partially or completely submerged. At the river Rhine, they could be observed on sites of the top to the low softwood zone with flooding durations of 77-100 % of the growing season. The combination of a cluster analysis with expert knowledge allowed the authors making a grouping into tolerance classes, including species for which no or only few data about flooding tolerance are available. Moreover, the problematic of defining prior classification ranges for each of the tolerance classes, being of particular complexity in the case of flooding tolerance, was bypassed by this technique.

Table 2: Flooding tolerance classes of 65 Central European tree and shrub species based on cluster analysis and expert knowledge (Glenz *et al.*, 2005; Chapter 3).

| Flooding tolerance classes | | | | |
|---|---|---|---|---|
| 1 <br> Very low | 2 <br> Low | 3 <br> Intermediate | 4 <br> High | 5 <br> Very high |
| *Fagus sylvatica* <br> *Picea abies* <br> *Acer pseudopl.* <br> *Abies alba* <br> *Tilia platyphyllos* <br> *Prunus avium* <br> *Larix decidua* <br> *Ilex aquifolium* <br> *Quercus petraea* <br> *Quercus pubescens* <br> *Juniperus communis* <br> *Crataegus laevigata* <br> *Prunus mahaleb* <br> *Amelancier ovalis* | *Acer platanoides* <br> *Carpinus betulus* <br> *Viburnum lantana* <br> *Corylus avellana* <br> *Robinia pseudo.* <br> *Castanae sativa* <br> *Berberis vulgaris* <br> *Crat. monogyna* <br> *Prunus spinosa* <br> *Tilia cordata* <br> *Ulmus glabra* <br> *Juglans regia* <br> *Aesculus hipp.* <br> *Malus sylvestris* <br> *Pinus sylvestris* <br> *Taxus baccata* <br> *Betula pendula* <br> *Sorbus aria* <br> *Sambucus nigra* | *Acer campestre* <br> *Ulmus minor* <br> *Lonicera xylosteum* <br> *Ligustrum vulgare* <br> *Rhamnus cathartica* <br> *Cornus sanguinea* <br> *Hipp. rhamnoides* <br> *Fraxinus excelsior* <br> *Quercus robur* <br> *Viburnum opulus* <br> *Populus alba* <br> *Populus tremula* <br> *Sorbus aucuparia* | *Alnus incana* <br> *Alnus viridis* <br> *Frangula alnus* <br> *Populus nigra* <br> *Prunus domestica* <br> *Prunus padus* <br> *Salix purpurea* <br> *Salix appendiculata* <br> *Salix caprea* | *Alnus glutinosa* <br> *Salix cinerea* <br> *Salix triandra* <br> *Salix viminalis* <br> *Salix elaeagnos* <br> *Salix daphnoides* <br> *Salix m. nigricans* <br> *Salix alba* <br> *Salix fragilis* <br> *Salix pentandra* |

## CONCLUSION

In this paper we considered flooding tolerance as the capacity of trees and shrubs to survive in anoxic conditions. We did not discuss the various species-specific life history strategies, such as the development of a high quantity of seeds, stem flexibility or the capacity of vegetative reproduction (Blom, 1999; Grubb, 1977), which can also be of importance for species maintenance in highly disturbed areas. However, based on this short review of species-tolerance to submergence, it is possible to formulate the following conclusions valid beyond the Central European context:

- Due to the complexity of interacting processes, the knowledge about flooding stress response of many tree and shrub species is quite sparse and, in some cases, contradictory. In the interest of simplicity, many of the field-studies carried out hitherto focused on the abiotic factors flooding duration and flooding depth, using absolute flooding depths instead of relative flooding depths, and neglected the importance of other abiotic factors, such as flooding frequency or the chemical

properties of the flood water. Nonetheless, the link between these abiotic factors and the physiological and metabolic processes exists and that they could be used to develop a more standardized method for estimating the effects of flooding on the different tree and shrub species. Such a method would entail the possibility to compare flooding stress response of species at different locations, taking survival or growth rates as reference.

- Field-studies for the purpose of quantifying tree damage in relation to flooding duration and depth were mainly initiated after large flooding events as tree-planting strategies needed to be adapted so as to avoid further economic losses in the managed riparian forests. Apart from such opportunistic studies, there has been no long-term monitoring of individual species response on quasi-natural rivers sites. Such long-term studies are essential not only to add and to improve existing knowledge, but also to develop a useful method for estimating the impact of flooding on species development. At present, laboratory experiments, which are mostly carried out on seedlings, provide important insights into the general mechanisms of flooding tolerance, but it is difficult to extrapolate results from them that are relevant to adult species or in-situ conditions. Therefore, in order to achieve a better and more comprehensive understanding of the flooding tolerance of tree and shrub species, laboratory experiments must be accompanied by field experiments.

- The use of the term flooding frequency might be ambiguous to characterise the increasing physiological stress due to recurring floods. The flooding frequency for a specific site corresponds to the number of times the site is flooded for a given time period. However, for a site with a flooding frequency of 10 years, it is possible to have floods in successive years or even within the same year. Therefore, in view of a more detailed evaluation of the impact of a specific flood on the flooding stress response due to limitations of the recovery time and the exposure to post-anoxic stress, the consideration of the 'time since last flooding' is more appropriate. Nevertheless, if only a rough characterisation of the stress due to flooding is required, particularly for sites with floods of short recurrence intervals, flooding frequency may present a good proxy to express this increasing flooding stress on tree and shrub species.

- From the point of view of modelling, the availability and quality of data on the relationship between the response to flooding of individual species and the responsible biotic and abiotic factors needs to be improved for modelling flooding stress response at a species level. However, tree and shrub species can be

classified into flooding tolerance classes considering by this implicitly the different morphological, physiological and metabolic adaptations (genetic constitution). Flooding stress response, which can be expressed by a decrease of shoot growth or survival rates, can then be modelled differently for each tolerance class. View the broad but still vague knowledge that exists of the effects of the abiotic factors on flooding stress response, a rule-based modelling approach based on fuzzy logic may be a possible way to proceed in the simulation of flooding stress on tree and shrub species.

Better knowledge of the flooding stress response of individual tree and shrub species as a result of more systematic investigations could improve the modelling of the impact of flooding on plant species, the planning of retention basins, the estimation of the economic repercussions of flooding on forestry or even the success of restoration projects. However one has to consider, that the success of restoration projects is not only evaluated by the diversity of tree and shrub species, but also by criteria, such as the establishment of a quasi-natural river dynamics, the presence of a shifting mosaic or natural physico-chemical conditions.

## ACKNOWLEDGEMENTS

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# Clustering of trees and shrubs into flooding tolerance classes – Case of Central European species

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# ABSTRACT

The ecological success of river restoration projects depends on the knowledge about the interacting driving-processes responsible for the riparian vegetation succession. The species-specific impact of submersion on the development of woody plants, *i.e.* flooding tolerance, is one of the dominant ecological processes responsible of the lowland riparian forest succession. An integral flooding tolerance classification of tree and shrub species found in the lowland and alpine riparian areas of Central Europe does not exist so far. This is primarily due to the lack of species-specific data and the complexity of the response to flooding stress. In this paper we intent to group the main Central European tree and shrub species into flooding tolerance classes using cluster analysis based on proxy-data for flooding tolerance, consisting of soil moisture preference, light preference, height to the mean water level and ability to develop morphological and anatomical adaptations to flooding. The clustering result is compared to existing qualitative and quantitative knowledge about flooding stress response to finally suggest a 3 and 5-scale flooding tolerance classification of Central European tree and shrub species. The use of a cluster analysis based on proxy-data allowed the inclusion of species for which no or only few data about flooding tolerance are available up to now and to bypass the problematic of defining prior classification ranges being of particular complexity for flooding tolerance. Furthermore, non-parametric regression analysis has been applied to verify the presence of moisture and light gradients in the riparian areas of Switzerland. The new flooding tolerance grouping of the main Central European tree and shrub species can find their use in modelling approaches, *e.g.* in riparian forest succession models adapted to riparian areas, and allow a better understanding of the relationship between species presence on a specific site and the environmental stress factors affecting it.

Keywords**:** flooding tolerance, clustering, Central Europe, woody species, proxy-data, non-parametric regression

## INTRODUCTION

The ecological success of river restoration projects depends on the knowledge about the interacting driving-processes (*e.g.* ecological, hydraulic) responsible for the riparian vegetation succession. The species-specific impact of submersion on the development of trees and shrubs is one of the dominant ecological processes responsible of the lowland riparian forest succession (McKnight *et al.*, 1981). Submersion tolerance, sometimes understood as flooding tolerance, is species specific, depending on biotic factors such as, genetic constitution, development stage, as well as on abiotic factors, such as flooding duration, depth or frequency (Glenz *et al.*, 2005; Chapter 2). Up to now, an integral flooding tolerance classification of tree and shrub species found in the lowland and alpine riparian areas of Central Europe does not exist. This is primarily due to the lack of species-specific data and the complexity of the response to flooding stress. Some relative rankings of a subset of species were indirectly done by describing processes in the field (*e.g.* Moor, 1958; Ehlers, 1960; Goettling, 1968), by analyzing results of experiments under controlled field conditions with seedlings (*e.g.* Frye and Grosse, 1992; Siebel *et al.*, 1998) or by evaluating tree damages after large flooding events (*e.g.* Dister, 1983; Späth, 1988; Biegelmeier, 2002). The existing flooding tolerance classifications relate (*e.g.* Prentice and Helmisari, 1991) or do not relate (*e.g.* Gulder, 1996) each tolerance class to a tolerance range of the specific stress the classification was initially based on (*e.g.* number of flooding days).

Classification of plant species into tolerance and indicator classes is common in plant ecology. Ellenberg (1996) developed for Central Europe an indicator system in which preference values for specific site conditions were attributed to each species. Similar indicator systems were developed by Hill *et al.* (1999) for Great Britain or by Landolt (1977) for Switzerland. These indicator values allow inferring site conditions by looking at the vegetation composition. On the other hand, classification in tolerance classes (*e.g.* drought tolerance, shade tolerance) is widespread in modelling of ecological processes, such as in forest succession models as JABOWA; see Botkin *et al.*, (1972).

However, as revealed in the review of Glenz *et al.* (2005; Chapter 2), a systematic classification of Central European tree and shrub species into flooding tolerance classes, based on their flooding stress response to the aforementioned abiotic factors can not be done properly. For many species detailed quantitative knowledge about these relationships is still missing or sparse. From a management point of view

it would be convenient to associate tolerated flooding characteristics (*e.g.* duration, relative depth) to flooding tolerance classes. However, this can hardly be done, as most of the existing investigations did not consider the same relevant factors at similar plant development stages, which may explain some differences in flooding stress response within a same species. Moreover, flooding stress response varies following the occurrence and extent of these abiotic factors. For instance, for a given tree height, a short, shallow (*e.g.* submergence of stem base) and regular flooding has not the same impact as a short, episodical but high flooding (*e.g.* complete submergence). Considering this, the use of mortality or damage rates in the classification process is problematic when not all of the important abiotic factors were recorded in a same manner to make the relation to the flooding stress response. Nevertheless, this information is highly valuable in adjusting a preliminary classification, which should not be based primarily on these abiotic factors but on data available for a large set of species indicating directly or indirectly (through proxy-data) flooding tolerance.

In this paper we intent to group the main Central European tree and shrub species into flooding tolerance classes using as basis a cluster analysis based on proxy-data for flooding tolerance, containing soil moisture preference, light preference, height to the mean water level and the ability to develop morphological and anatomical adaptations to flooding. The clustering result is compared to existing qualitative and quantitative knowledge about flooding stress response, taking into account existing flooding tolerance classifications, to finally suggest a 3 and 5-scale flooding tolerance classification of Central European tree and shrub species. Cluster analysis based on proxy-data allows determining groups of species with similar flooding tolerance characteristics including species for which no or only few data about flooding tolerance are available up to now. Moreover it allows bypassing the problem of defining prior classification ranges being of particular complexity for flooding tolerance. We suppose in this paper that soil moisture preference can be a surrogate of flooding tolerance. It can be expected that moisture preferring species are physiologically, morphologically or metabolically more adapted to an excess of water compared to xeric species. Bedinger (1978) claims the relationship between the plant distribution in floodplains and a soil moisture gradient, and implicitly by this, the preference of a plant species for moist conditions. Next to the soil moisture gradient, we suppose that floodplains reveal also a light availability gradient. From the flooding disturbed to the non-flooding disturbed sites, canopy is generally getting closer and species regeneration is affected by the interaction of the two life-historical traits, shading and flooding tolerance (Hall and Hardcombe, 1998). In the regularly flooding disturbed areas mainly pioneer species that require a high light availability can be

found. Apart the fact that these species generally have higher growth rates allowing them to avoid more rapidly complete submergence (Blom, 1999), we consider that they develop more easily flooding related adaptations (Siebel and Blom, 1998) – as flooding stress response is not only the expression of flooding depth, but also of flooding duration, flooding frequency and flooding timing (Glenz *et al.*, 2005; Chapter 2). Blom (1999) outlined the relationship between the light requirements of tree seedlings and their flooding tolerance. Species with a low shading tolerance (*e.g. Salix viminalis*) are supposed to be more flooding tolerant then species with a high shading tolerance (*e.g. Alnus pseudoplatanus*). To express the soil moisture preference and the light preference of the considered Central European tree and shrub species, two different indicator systems have been used. The Ellenberg indicator system (Ellenberg, 1996) was developed for Central Europe on a 9-point scale, whereas Landolt (1977) estimated a similar indicator on a 5-point scale for the specific conditions in Switzerland. As a third variable for the proxy-data, the height over the mean water level is selected to express flooding tolerance. We consider that the probability being flooded increases the more a site is close to the mean water level and that the woody plant species need to be adapted to such stress in order to survive. Hall and Hardcombe (1998) outlined in their study that elevation is a surrogate of flooding tolerance. The final variable for the proxy-data considers the ability of the tree and shrub species to respond to flooding stress by the three important morphological/ anatomical adaptations – adventitious roots, hypertrophied lenticels and aerenchyma (Kozlowski, 1997). Following Hook and Brown (1973) the most tolerant tree species generally show also the most morphological and physiological adaptations. However, one has to be aware that some species may have adaptations which simply were not described yet. In this sense, the use of a set of variables of different nature in the proxy-data allows to improve the validity of the clustering and to determine more accurately the relative position of each species within the tolerances of the others.

To verify whether in the remaining natural and quasi-natural riparian areas of Switzerland really soil moisture and a light availability gradients exist, the relationship between the abundance of moist soil and light preferring species and their height over the mean water level is analyzed using non-parametric regression (Bowman and Azzalini, 1997). An increase of soil moisture and light preferring species approaching the mean water level implicitly indicates the presence of these gradients (Bedinger, 1978; McNight *et al.*, 1981).

Classifying tree and shrub species into flooding tolerance classes, implicitly integrates morphological, physiologic and metabolic adaptations to flooding. Therefore, the suggested flooding tolerance classifications can find their use in

modelling approaches, *e.g.* in riparian forest succession models adapted to riparian areas, and allow a better understanding of the relationship between species presence on a specific site and the environmental stress factors (*e.g.* drought, flooding, shade) affecting it.

## METHOD

## Central European tree and shrub species data

For this study sixty-five Central European tree and shrub species were selected. Most have been recorded in alluvial sites in Switzerland (Roulier, 1998).

*a. Soil moisture preference of tree and shrub species (HIL, HIE)*

To represent the soil moisture preference of tree and shrub species, Landolt's (1977) H-indicator (1,...,5) and Ellenberg's (1996) H-Indicator (1,…,9), have been used. In what follows they will be abbreviated by HIL and HIE. The analysis of the relationship between the soil moisture preference and the height to the mean water level was performed based on the weighted soil humidity indicator values of Landolt (1977) evaluated on 443 vegetation relevees in alluvial sites of Switzerland (Roulier, 1998). These sites are all part of the national riparian vegetation inventory of Switzerland, which records the remaining quasi-natural and natural riparian areas of Switzerland.

*b. Light requirements of tree and shrub species (LIL, LIE)*

To represent the light requirements of tree and shrub species, Landolt's (1977) L-indicator (1,...,5), LIL, and Ellenberg's (1996) L-Indicator (1,…,9), LIE, expressing the light preferences of a species at a sapling stage, have been considered. We assume that these light preference indicators express inversely species tolerance to shading. The analysis of the relationship between the light preferences and the height to the mean water level was performed based on the previously described method and applied to the same 443 vegetation relevees.

*c. Height over mean water level (HMWL)*

For the analysis herein, we selected 98 vegetation relevees of alluvial sites in Switzerland (Roulier, 1998), based on their location (all located below 700 m.a.s.l.) and clear indications of regular flooding. Note that the height over the mean water level (HMWL) was estimated through observation. For all of the inventoried species, we summed up the corresponding abundances and normalised at heights of 0.0-0.5 m (*n=25*), 0.5-1.0 m *(n=29)*, 1.0-1.5 m *(n=8)*, 1.5-2.0 m *(n=18)*, 2.0-2.5 m *(n=3)*, 2.5-

3.0 m *(n=5)*, 3.0-4.0 m *(n=6)* and >4.0 m *(n=4)* over the mean water level. As the abundances closer to the mean water level are more expressive concerning flooding tolerance, the summed abundances have been weighted (the closer to the mean water level, the higher the weight). Finally, a tolerance class (1,...,8; non-tolerant to tolerant) has been associated to each species based on the HMWL for which the highest weighted abundance was calculated.

*d. Flooding stress adaptations (FLDA)*
Indications of anatomical and morphological flooding stress adaptations (FLDA) have been considered based on the review of Glenz *et al.* (2005; Chapter 2). Following Kozlowski (1997) the morphological and anatomical adaptations, as adventitious roots, hypertrophied lenticels and aerenchyma are the three important flooding stress adaptations. Data about presence of adventitious roots, lenticels, aeranchyma were collected for each of the considered tree and shrub species and summed up to express the number of considered adaptations each species develops.

*e. Quantitative and qualitative indications of flooding tolerance*
The clustering result was compared to and adjusted by available qualitative descriptions of flooding tolerance (*e.g.* Dister, 1983; Ehlers, 1960; Ellenberg, 1996; Goettling, 1968; Kramer, 1987; Moor, 1958; Wendelberger, 1973) and data indicating relative tolerance classes (*e.g.* Bernatzky, 1978; Gulder, 1996; Prentice and Helmisari, 1991) and quantitative data, mostly studies which put in relation flooding duration and height to tree injury indications or tree death (*e.g.* Biegelmaier, 2002; Dister, 1983; Siebel and Blom, 1998, Siebel *et al.*, 1998; Späth, 1988; Späth, 2002).

## Analytical methods

*Non-parametric regression analysis*
To analyse the relationship between the soil moisture preference and the height to the mean water level, and the relationship between the light preference and the height to the mean water level, we applied the usual hypotheses for testing for no effect, *i.e.* null-hypothesis $H_0$ posits no effect; using the S-Plus library sm following Bowman and Azzalini (1997). We compared the hypotheses $H_0$: $E(y_i) = \mu$ and $H_1$: $E(y_i) = m(x_i)$, where for *n* data points *(x_i,y_i)*, $\mu$ corresponds to the mean and $m(\cdot)$ to an unknown smooth function. The standard approach from classical linear models was extended by Azzalini *et al.* (1989) to the non-parametric setting. Applied to our case, we compare the null hypothesis ($H_0$) that HIL does not change in function of HMWL,

being equal to the mean value of HMWL ($\mu$), with the alternative hypothesis ($H_1$) that there is a non-linear relationship between the two variables. By placing a reference band around the null (reference) model, indicating where the non-parametric regression curve should lie under the null hypothesis, the difference between the non-parametric and the null model can be graphically followed up in order to decide about rejection or non-rejection of $H_o$. If the curve exceeds the band the null and non-parametric models are more than two standard errors apart (under the assumption that the null model is correct). Finally, by plotting the *p*-value over a wide range of the smoothing parameter *h* (controlling the level of smoothness of the fitted curve), known as significance trace, allows to indicate the influence of *h* changes on the significance of the test. For more details we refer to Bowman and Azzalini (1997).

*Cluster analysis and classification procedure*

The first step of the classification procedure is the cluster analysis based on the unweighted variables HIL, HIE, LIL, LIE, HMWL and FLDA. The determined groups are associated to flooding tolerance classes by using principal component analysis (PCA) and expert knowledge, taking into account the above-cited quantitative and qualitative data.

The cluster analysis integrated 42 tree and shrub species, as only for these species a complete data set could be prepared. Species with missing data are per default omitted in this clustering method. Therefore, the other 23 species were added to the existing grouping using expert knowledge.

As our main concern is to obtain the main structure of the data, we used divisive hierarchical clustering, based on the cited five variables using the S-Plus clustering function diana. For details about this method see Kaufman and Rousseeuw (1990). The hierarchical method yields an entire hierarchy of clusterings for the given data set represented by a dendrogram. The desired main structure is then obtained by focusing on its upper levels. Division is started considering all of the points as one cluster. This is then split into components by selecting at each step the cluster C with the largest diameter $d(C) := \max_{i,j \in C} d(i,j)$, until each object is separated. The diameter of a cluster is the largest dissimilarity between any two of its objects. The dissimilarity matrix has been calculated using Euclidean distances for *d(i,j)*. The vertical coordinate of the resulting dendrogram corresponds to where a branch splits in two equals the diameter of that cluster before splitting. As the variables are not measured at the same scale they were standardized first. As a clustering quality measure, we used the divisive coefficient (DC), which indicates the amount of clustering structure found in the data. The DC is obtained by denoting for each object *i*, the diameter of the last cluster C, *d(C),* to which it belongs (before being split off as a single object),

divided by the diameter of the whole dataset. Finally the DC is defined as the average of all *d(C)*. A DC of one corresponds to a clear cluster structure

The final classification into three and five tolerance classes was performed adapting the clustering result through expert knowledge and by referring also to the available qualitative descriptions and data indicating relative tolerance classes, as well as on quantitative data of tolerated flooding durations and flooding depths. To underline the results found in the cluster analysis and to investigate in the importance of the variables HIL, HIE, LIL, LIE, HMWL and FLDA a principal component analysis (PCA) with resulting biplot is displayed.

# RESULTS AND DISCUSSION

## Lateral gradient analysis

Figure 1 (a) shows the relationship between HMWL and HIL for the 443 vegetation relevees in alluvial sites of Switzerland. We can determine that the superposed non-parametric regression curve with smoothing parameter *h*=1 exceeds the reference band at every position, underlining the evidence that there is a relationship between the variables HIL and HMWL. Figure 1 (b) gives the p-value as a function of the smoothing parameter *h*, *i.e.* the significance trace, indicating that even by varying *h* the test remains significant. Increasing moisture-preferring species approach the mean water level, indicating by this the presence of a soil moisture gradient, which to a certain degree can be attributed to regular flooding events bringing along higher groundwater levels (Tiner, 1996). Considering that the indicators values of Ellenberg and Landolt allow inferring site conditions, our result confirms the concept of Whittaker (1967) and its application to the riparian areas of Switzerland in regard of soil moisture (Bedinger, 1978). Indeed, Whittaker's concept claims, that species population are distributed along environmental gradients each according to its own physiology and genetic pattern.

(a)
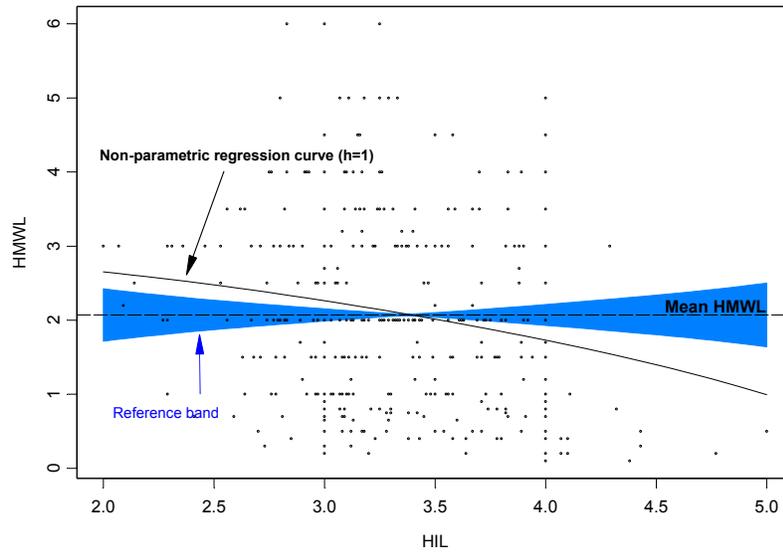


(b)



Figure 1: (a) HMWL versus HIL with superposed reference band for the no-effect model (smoothing parameter *h*=1), (b) Significance trace: p-values as a function of the smoothing parameter *h* for the relationship between HMWL and HIL.

Figure 2 (a) shows the relationship between HMWL and the weighted light indicator LIL for the 443 vegetation relevees in alluvial sites of Switzerland. We can determine again that the superposed non-parametric regression curve with a smoothing parameter of *h*=1.5 exceeds the reference band at every position, underlining the evidence that there is a relationship between the variables HMWL and LIL. The more we approach the mean water level the more light-demanding species can be found, revealing the presence of a light gradient. The significance trace in Figure 2 (b) indicates again that even by varying *h* the test remains significant. Considering that elevation can be used as surrogate of flooding tolerance (Hall and Hardcombe, 1998), the two results underline that soil moisture and light preference of plant species are relevant to proxy-data of flooding tolerance.
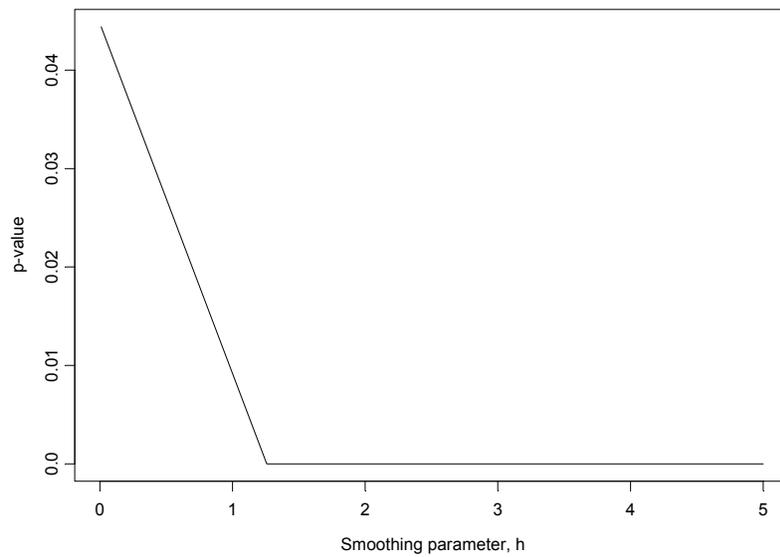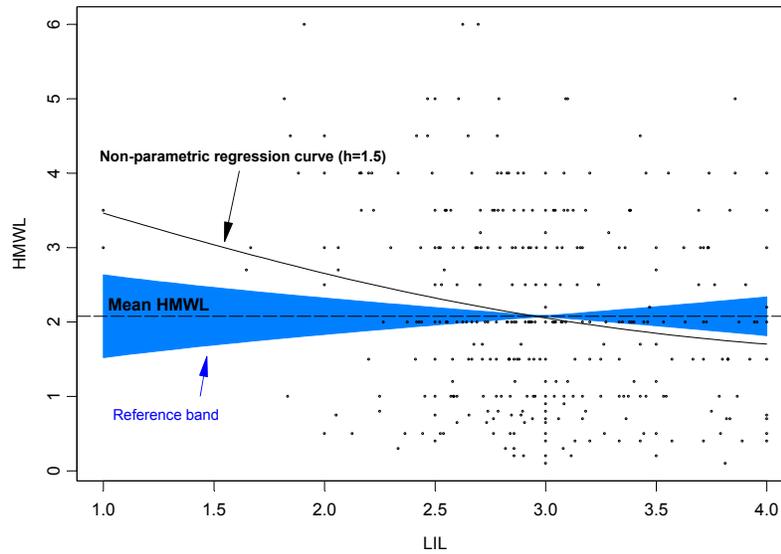
(a)



(b)
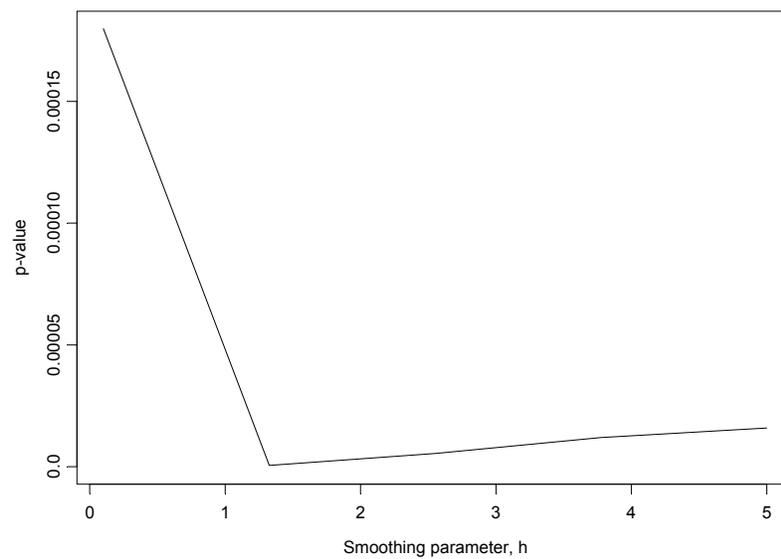


Figure 2: (a) HMWL versus LIL with superposed reference band for the no-effect model (smoothing parameter *h*=1.5), (b) Significance trace: p-values as a function of the smoothing parameter *h* for the relationship between HMWL and LIL.

## Cluster analysis result

On Figure 3 the dendrogram of the divisive hierarchical cluster analysis of 42 European tree and shrub species based is displayed. At height 8, the clustering reveals three (A, B, C) and at height 6 seven different groups, indicated by (1,…,4, 5\*, 5\*\*, 5\*\*\*). Moreover, the divisive coefficient of 0.78 indicates a good clustering structure.

Dendrogram - Flooding tolerance of Central European tree and shrub species
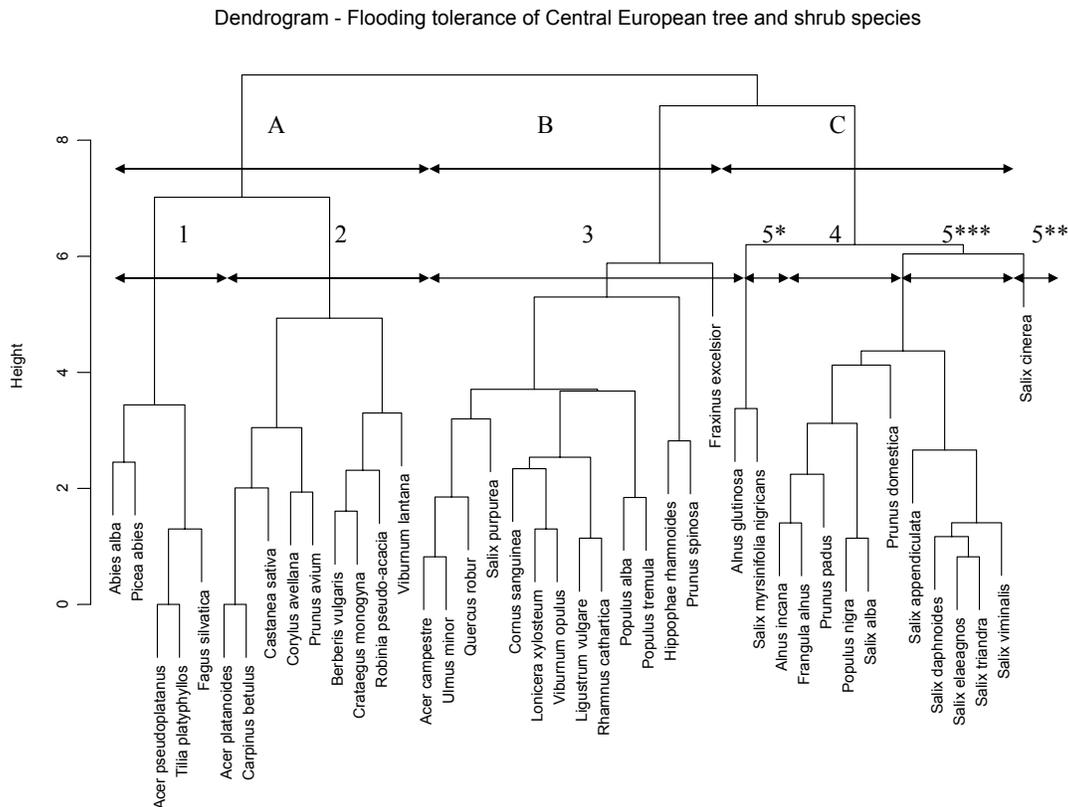


Figure 3: Divisive hierarchical clustering based on 42 Central European
tree and shrub species.

Figure 4 presents the biplot for the 42 species based on the correlation matrix. In Table 1 the loadings of the derived variables and the cumulated percentage of the explained variance can be found. One can see that the first two principal components explain 67.75 % of the variance. Moreover, Table 1 reveals that the first principal component is mainly dominated by the soil humidity indicators (HIL, HIE), whereas in the second principal component the light indicators (LIL, LIE) play an important role.

51
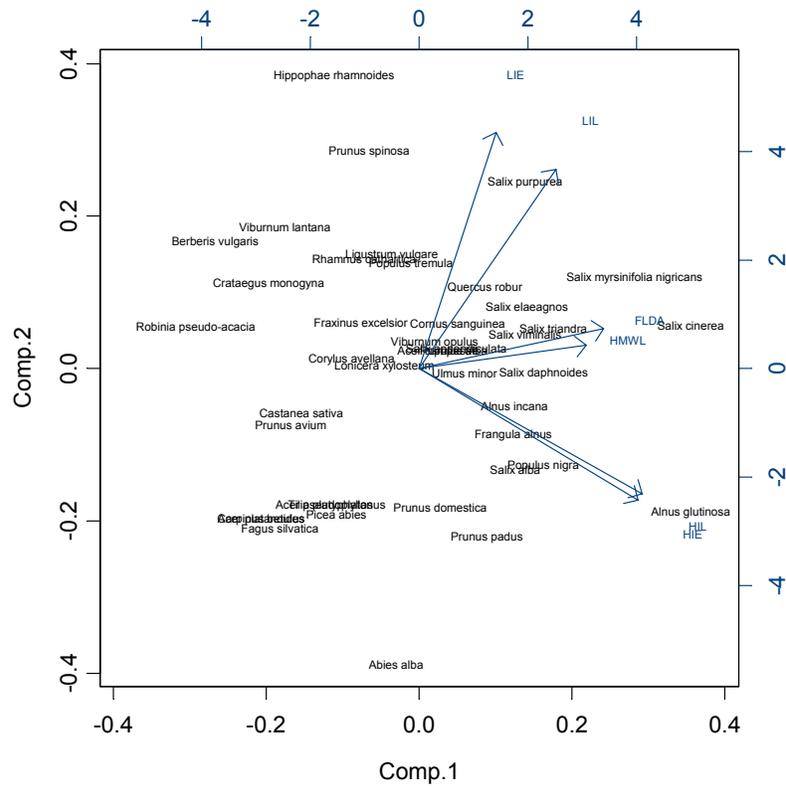
Figure 4: Biplot for the 42 species based on the correlation matrix.

Table 1: Principal component's (PC) loadings of the derived variables and cumulated percentage of the variance explained.

| Variable | PC 1 | PC 2 | PC 3 | PC 4 | PC 5 | PC 6 |
|---|---|---|---|---|---|---|
| LIL | 0.319 | 0.551 | 0.318 | 0.000 | 0.695 | 0.000 |
| LIE | 0.179 | 0.654 | 0.219 | -0.195 | -0.670 | 0.000 |
| HIL | 0.520 | -0.346 | 0.304 | 0.000 | -0.149 | 0.699 |
| HIE | 0.510 | -0.364 | 0.321 | 0.000 | 0.000 | -0.709 |
| HMWL | 0.389 | 0.000 | -0.640 | -0.642 | 0.148 | 0.000 |
| FLDA | 0.430 | 0.111 | -0.495 | 0.731 | -0.152 | 0.000 |
| Cumulated % of variance explained | 39.55 | 67.75 | 83.97 | 93.18 | 98.08 | 100.00 |

# Grouping into flooding tolerance classes

*A. Grouping into three tolerance classes*

Based on the biplot and on the available qualitative and quantitative data, we are able to determine that group A represents non-tolerant species, group B aggregates mid-tolerant species and group C flooding tolerant species. In group A species like *Fagus sylvatica* can be found which are known to tolerate only few days of flooding (Späth, 1988) and considered as being flooding intolerant (Bernatsky, 1978; Prentice and Helmisaari, 1991) or having a low to very low flooding tolerance (Gulder, 1996; Ehlers, 1960; Späth, 2002). The same holds for *Prunus avium* (Gulder, 1996; Ehlers, 1960; Späth, 1988; Späth, 2002) and *Acer pseudoplatanus* (Bernatsky, 1978; Gulder, 1996). Dister (1985) noticed that *Fagus sylvatica,* but also *Acer pseudoplatanus* and *Acer platanoides* are not typical riparian species as they tolerate only several days of flooding. The two only gymnosperms, *Abies alba* and *Picea abies,* can also be found in (A), confirming the observations by Kozlowski and Pallardy (1997) that gynmnosperms in general have a lower flooding tolerance than angiosperms. Next, in the mid-tolerant group B, species like *Fraxinus excelsior, Populus tremula, Acer campestre, Quercus robur* can be found. Gulder (1996) considered *Fraxinus excelsior* being a mid-flooding tolerant species and *Quercus robur* a mid- to high tolerant species. Of the three *Acer* spp., *Acer campestre* tolerates best longer floodings (Späth, 1988), which is reflected by the clustering result. According to Ehlers (1960) *Populus tremula* (B) has a lower flooding tolerance compared to *Populus nigra* (Goettling, 1968), associated to group C. Note that Gulder (1996) considered *Populus tremula*, together with *Populus alba*, group B, as being even low flooding tolerant. The association of *Salix purpurea* to group B is questionable. The biplot illustrates that the association of *Salix purpurea* in group B can be explained by its lower soil moisture indicator values compared to the other *Salix* spp., however *Salix purpurea* is known tolerating long flooding periods and even complete flooding (Ehlers, 1960; Moor, 1958). In this regard, *Salix purpurea* should be associated to group C. For the shrub species *Lonicera xylosteum*, *Rhamnus cathartica*, *Prunus spinosa* and *Hippophae rhamnoides* quantitative or qualitative indications about flooding tolerance is sparse. The biplot reveals clearly that *Hippophae rhamnoides* and *Prunus spinosa* are species with high light requirements, found mainly on dry soils. The presence of these species in group B is mainly explained by their very high light requirement and the few flooding adaptations, compared to the species of group A. Taking into account the observation of Moor (1958), *Hippophae rhamnoides* can be found on sites which at mean water level may partially be flooded and at high flooding events completely submerged. Hence the clustering result seems to be

confirmed. However, *Prunus spinosa* is generally found on rarely flooded sites (Ehlers, 1960), imposing a relocation of *Prunus spinosa* to a lower flooding tolerance class. Note that Moor (1958) observed establishment of *Lonicera xylosteum*, *Cornus sanguinea* and *Viburnum opulus* seedlings at the height of the mean water level in a Salicetum triandro-viminalis association, however with only a poor successful development.

Group C is composed mainly by flooding tolerant *Salix* spp., such as *Salix alba* (Dister, 1983; Gulder, 1996; Späth, 1988) and *Alnus* spp., such as *Alnus glutinosa* (Späth, 2002) and *Alnus incana* (Gulder, 1996), together with *Prunus padus, Frangula alnus* and *Prunus domestica.* Following Elhers (1960) *Prunus padus* can be found on fresh to humid soils, tolerating flooding. Bernatztky (1991) adjucated to *Prunus padus* to be flooding tolerant, whereas Gulder (1996) considered *Prunus padus* being even highly flooding tolerant. In opposition, no indications of flooding tolerance could be found for *Prunus domestica,* which based on the biplot, has similar ecological requirements as *Prunus padus.*

### B. Grouping into five tolerance classes

At a height of 6, the dendrogram displays two new larger splits for group A and four for group C. Based on the biplot and the available quantitative and qualitative data, group 1 is supposed to represent a very low flooding tolerance group and group 2 a low tolerance group. On the other hand, group 4 represents a high flooding tolerance group, whereas group 5* and group 5**, composed by a single species, can be aggregated together with group 5*** to a very high tolerance group 5. For instance, the coniferous species *Abies alba* and *Picea abies*, as well as the very low flooding tolerant species *Fagus sylvatica* can be found in group 1. *Acer platanoides* which following Gulder (1996) is more tolerant than *Acer pseudoplatanus*, in group (2), together with *Carpinus betulus* tolerating flooding up to several weeks (Späth, 1988; Späth, 2002) and *Viburnum lantana*. *Viburnum lantana* (2) is less tolerant than *Viburnum opulus* (3) found on sites which are regularly flooded (Goettling, 1968). However, *Prunus avium* known being very low flooding tolerant (Ehlers, 1960; Gulder, 1996; Späth, 1988) was also associated to group 2. Next, group 4 is composed by species like *Salix appendiculata*, *Alnus incana* but also by the very flooding tolerant species *Salix alba* (Ehlers, 1960; Gulder, 1996)*,* tolerating flooding during the entire growing season (Dister, 1983; Späth, 1988). In opposition, in group 5 we find *Salix viminalis* known to be insensitive to flooding (Ehlers, 1960), *Salix cinerea* preferring sites with year-round submergence by groundwater (Lange and Lecher, 1993), *Salix daphnoides* which following Gulder (1996) has very high tolerance to flooding (together with *Salix fragilis*).

The described clustering allowed us to group Central European tree and shrub species with similar flooding tolerance characteristics and also to determine, based on the biplot and the available quantitative and qualitative data, their corresponding relative flooding tolerance. Based on this, 3- and 5-level flooding tolerance classifications were formulated for the 42 tree and shrub species; see Table 1. The classification can be considered as relative in the sense, that the clustering is based on proxy-data which are not directly related to absolute values of tolerated flooding durations or flooding depths. Because of this, the classification result expresses only species vulnerability to flooding in relation to others. It is obvious that within the species of a same tolerance class vulnerability may still differ (particularly within group B) but we suppose to a lesser extent compared to the next higher or next lower tolerance class. Nevertheless, apart from *Prunus avium* and *Prunus spinosa,* which need to be reattributed to a lower and *Salix purpurea* and *Salix alba* to a higher tolerance class, the relative flooding tolerance classifications are consistent with the quality and availability of the actual data about Central European tree and shrub species.

The remaining 23 tree and shrub species, which contained missing data, have been classified based on Ehlers (1960), Goettling (1968), Gorzelak (2000), Lange and Lecher (1993), Prentice and Helmisaari (1991), Späth (1988) and others. Out of these 23 species, some were classified taking the cluster result as reference. For example *Ulmus glabra* has been classified in group 2 as following Gulder (1996) *Ulmus minor* which is in group 3 is supposed to be more flooding tolerant, similar for *Tilia cordata* which is much more tolerant then *Tilia platyphyllos.* The final classification into flooding tolerance classes is displayed in Table 2.

Table 2: Determined tolerance classes of 65 Central European tree and shrub species. Classification into three (A, B, C) and five (1,…,5) tolerance classes. In brackets the data-based clustering group at height 6. Changes issued from expert knowledge are bold-faced.

| Flooding tolerance classes | | | | |
|---|---|---|---|---|
| **A** | | **B** | **C** | |
| 1 | 2 | 3 | 4 | 5 |
| *Fagus sylvatica (1)* | *Acer platanoides (2)* | *Acer campestre(3)* | *Alnus incana (4)* | *Alnus glutinosa (5)* |
| *Picea abies (1)* | *Carpinus betulus (2)* | *Ulmus minor* (3) | *Prunus domestica (4)* | *Salix cinerea (5)* |
| *Acer pseudopl.(1)* | *Viburnum lantana (2)* | *Lonicera xylosteum* (3) | *Prunus padus* (4) | *Salix triandra (5)* |
| *Abies alba (1)* | *Corylus avellana (2)* | *Ligustrum vulgare* (3) | *Salix appendiculata (4)* | *Salix viminalis (5)* |
| *Tilia platyphyllos (1)* | *Robinia pseudo. (2)* | *Populus tremula (3)* | *Frangula alnus (4)* | *Salix elaeagnos (5)* |
| ***Prunus avium (2)*** | *Castanae sativa (2)* | *Rhamnus cathartica (3)* | *Populus nigra (4)* | *Salix daphnoides (5)* |
| | *Berberis vulgaris (2)* | *Cornus sanguinea (3)* | ***Salix purpurea (3)*** | *Salix m. nigricans (5)* |
| | *Crat. monogyna (2)* | *Hipp. rhamnoides (3)* | | ***Salix alba (4)*** |
| | ***Prunus spinosa (3)*** | *Fraxinus excelsior (3)* | | |
| | | *Quercus robur* (3) | | |
| | | *Viburnum opulus (3)* | | |
| | | *Populus alba (3)* | | |
| **Added species based on expert knowledge and literature data** | | | | |
| *Larix decidua (-)* | *Tilia cordata (-)* | *Sorbus aucuparia (-)* | *Alnus viridis (-)* | *Salix fragilis (-)* |
| *Ilex aquifolium (-)* | *Ulmus glabra (-)* | | *Salix caprea (-)* | *Salix pentandra (-)* |
| *Quercus petraea (-)* | *Juglans regia (-)* | | | |
| *Quercus pubescens* (-) | *Aesculus hipp.( -)* | | | |
| *Juniperus communis (-)* | *Malus sylvestris (-)* | | | |
| *Crataegus laevigata (-)* | *Pinus sylvestris (-)* | | | |
| *Prunus mahaleb (-)* | *Taxus baccata (-)* | | | |
| *Amelancier ovalis (-)* | *Sorbus aria (-)* | | | |
| | *Sambucus nigra (-)* | | | |
| | *Betula pendula (-)* | | | |

Tolerance classifications often indicate tolerance ranges of the specific stress the classification was initially based on (*e.g.* number of flooding days). However, in case of the flooding stress, response is not simply the consequence of one factor but of a combination of several abiotic (*e.g.* flooding duration, relative flooding depth) and biotic (*e.g.* development stage) factors (Glenz *et al*., 2005; Chapter 2). Following the combination of these factors the absolute tolerated ranges, generally expressed in days or depth, may vary form one site to another and are therefore spatially-specific. We suppose however, that the determined classification is not spatially associated and conserves the response pattern (vulnerability) at changing flooding stress conditions.

Despite the limitations cited before, we try to synthesize tolerated flooding characteristics of each of the tolerance classes, particularly for group A, B and C; see Table 3. The indicated tolerated flooding durations and the association of the tolerance classes to the lateral vegetation zonation are based on studies at the river

Rhine (Kramer, 1987; Späth, 1988; Späth, 2000, Michiels and Aldinger, 2002). Note that the indications have been strongly simplified.

Table 3: Simplified representation of flooding tolerance classes characteristics for tolerance class (A, B, C) and (1, …,5).

| Simplified representation of flooding tolerance classes characteristics | | | | |
|---|---|---|---|---|
| **A** Low flooding tolerance | | **B** Intermediate flooding tolerance | **C** High flooding tolerance | |
| Hardwood species presenting quasi no morphological and physiological adaptations to flooding. Tolerating soil submersion, less partial submersion but not complete submersion. Sensible to irregular and extreme floods, however more tolerant to regular but low floods. Found on sites of the top to medium hardwood zone with flooding durations of 5-35 % of the growing season. | | Mix of softwood and hardwood species, in which some species develop adaptations to flooding. Tolerating partial submersion, but less complete submersion. Species tolerating medium floods. Found on sites of the medium to the low hardwood zone with flooding durations 36-60 % of the growing season. | Softwood species with morphological and physiological adaptations to flooding. Tolerating partial submersion and complete submersion. Tolerant to irregular floods and extreme floods. Found on sites of the top to the low softwood zone with flooding durations 61-100 % of the growing season. | |
| **1** Very low | **2** Low | **3** Intermediate | **4** High | **5** Very high |
| Species tolerating only short floods. Found on sites of the top hardwood zone with flooding durations of 5-20 % of the growing season. | Species tolerating short to medium duration of floods. Found on sites of the medium hardwood zone with flooding durations of 21-35 % of the growing season. | | Species tolerating long floods. Found on sites of the top softwood zone with flooding durations 61-76 % of the growing season. | Species tolerating very long floods. Found on sites of the top to the low softwood zone with flooding durations 77-100 % of the growing season. |

## Limitations of grouping procedure

The reasons why some species needed to be associated to other tolerance classes may rely first, in a lack of accuracy of the species-specific ecological requirements of the proxy-data (*e.g.* LIL, LIE), or second, in a over- respectively underestimation of the significance of the proxy data to express flooding tolerance (*e.g.* soil moisture preference versus light availability preference), or third, in a general lack of knowledge of plant physiology and anatomy (*e.g.* type and number of adaptations developed). Moreover it is difficult to evaluate whether the used surrogates for flooding tolerance, particularly HMWL and LIE/LIL, dominantly express the aspect of

tolerance to submersion and not other life historical strategies (*e.g.* vegetative reproduction) responsible for species presence close to the mean water level. Nevertheless, the clustering procedure based on proxy-data allowed us to determine the main flooding tolerance groups by focusing on the upper levels of the dendrogram. Moreover, aggregation of species into similar groups is performed by data-driven statistical algorithms, therefore not requiring a prior definition of classification ranges. However, based on the above-mentioned limitations and the fact that, the incorporation of new species-specific insights by adapting proxy-data (*e.g.* increase of number of adaptations) may change clustering result particularly at lower levels of the dendrogram (clustering result is more robust at upper levels), it would not have been reasonable to distinguish more tolerance groups.

## CONCLUSION

The application of a proxy data-based classification, combining statistical clustering procedure with expert knowledge, as well as qualitative and quantitative data about flooding stress response, allows suggesting a relative flooding tolerance classification consistent with the quality and availability of the actual data about Central European tree and shrub species. It allowed integrating species for which no field observations concerning flooding stress response were available and also bypassing the problematic of defining classification ranges being of particular complexity for flooding tolerance. However, the outlined limitations of using proxy-data indicate the importance of systematic studies furnishing comparable quantitative data about flooding stress response. Up to now, quantitative measurements relating for example flooding depth and duration with species survival result sometimes in differing and even contradictory observations mainly due to unilateral investigations of the responsible abiotic and biotic processes. Finally, grouping of tree and shrub species into flooding tolerance classes is not only useful for modelling approaches, for example in river restoration projects or the planning of retention basins, but simply for a better understanding of the relationships between the species presence on a specific site and the environmental stress factors (*e.g.* drought, flooding, shade) affecting it.

## ACKNOWLEDGEMENTS

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# CHAPTER 4

# Modelling flooding stress response of tree species using fuzzy logic

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# ABSTRACT

Within the driving-processes responsible for riparian forest dynamics, the species-specific impact of flooding on the development of woody plants plays a key role – particularly for lowland rivers. Only a few of the currently used forest succession models include flooding stress response of trees. Generally, these approaches consider only partially the main responsible biotic and abiotic factors implicated in species response to flooding in riparian areas. This situation is mainly attributed to unilateral investigations of the flooding tolerance processes and the related abiotic and biotic factors. In this sense, the relation between flooding stress and growth is still a field of ongoing investigations and process-based modelling based on physiological or metabolic processes cannot be done properly. The present research suggests an approach to model tree response to flooding using the fuzzy set theory, in attempt to use the broad but still vague knowledge about flooding stress. The application is illustrated for the case of Central European species. Flooding stress response to the abiotic factors, duration, depth and frequency of flooding, differs following five flooding tolerance classes and is expressed by means of a growth factor limiting optimal tree growth. Therefore, the flooding tolerance model can be integrated into more complex forest succession models, such as Gap models, adapted to riparian areas. A forest succession model including flooding tolerance modelling can present a helpful tool in the decision-making process of large lowland river restoration projects, by illustrating riparian forest dynamics at specific river corridor designs.

Key words: flooding tolerance, modelling, fuzzy logic, riparian forest, GAP model, river restoration

## INTRODUCTION

Vegetation zonation in lowland riparian areas depends particularly on the flooding tolerance of the respective tree species (Bedinger, 1971; Siebel and Blom, 1998). Flooding tolerance is understood in this research as the capacity to survive in anoxic conditions (Hook, 1984). The lack of oxygen affects vital physiological and metabolic pathways which can induce various plant responses, including injury, inhibition of seed germination, vegetative and reproductive growth, changes in plant anatomy, promotion of early senescence and mortality. However, the most significant and usual symptom is a decline in shoot growth (Dickson et al., 1965; Kozlowski, 1984; Frye and Grosse, 1992; Ewing, 1996; Blom et al., 1994). Within the driving-processes responsible for riparian forest dynamics, the impact of flooding on tree species, in relation to their flooding tolerance, plays a key role – particularly for lowland rivers (McKnight et al., 1981). The review by Glenz et al. (2005a; Chapter 2) suggests that flooding tolerance is the expression of physiological and morphological adaptations of tree and shrub species to flooding stress, but which on the other hand is strongly related to non species-specific abiotic (e.g. flooding depth, duration, frequency and timing of flooding, etc.) and biotic factors (e.g. development stage). Finally, these factors determine the extent of growth reduction or the death of the individual trees considered.

During recent years a large number of top-down or bottom-up vegetation models have been developed differing in time scale and spatial extent (e.g. global models, physiological models). These models can be attributed to two major concepts: the static equilibrium vs. the dynamic transient concept (Bolliger et al., 2000). In dynamic transient vegetation models vegetation is never in equilibrium, therefore vegetation dynamics are considered on patches, where each is interpreted as a time and space-specific transient result of previous disturbances. The dynamic transient concept is coherent with the philosophy of for example the distribution-based forest succession models or the gap models. They simulate the succession by modelling the interrelationships among vegetation elements, for example within a forest stand, including process-based approaches that account for competition as well as for the interaction with the abiotic environment. They are therefore well suited for examining vegetation response to changing environmental conditions because the expression of plant response to the environment is not limited to reproducing present day conditions (Shugart and Prentice, 1992). Within the existing forest succession models developed since the mid-1970's, only a few of the JABOWA type (Botkin et al., 1972) have included flooding stress response of trees. Pearlstine et al. (1985) developed a bottomland hardwood succession model (FORFLO) to study the impact

of an altered hydrologic regime on the growth and succession of coastal forested floodplain in South Carolina, US. The model SWAMP (Phipps, 1979) aimed to simulate the forest vegetation dynamics of southern wetlands in Arkansas, US. Both of these approaches consider only partially the main biotic and abiotic factors implicated in species response to flooding in riparian areas. Moreover, tolerated flood ranges/factors have been set based on species response observed at a single river, the White River (Bedinger, 1971). Accurate information about flooding stress response is quite sparse and sometimes even contradictory, mainly attributed to unilateral investigations of the flooding tolerance processes and the related abiotic and biotic factors (Glenz et al., 2005a; Chapter 2). In this sense, the relation between flooding stress and growth is still a field of investigation, and process-based modelling based on physiological or metabolic processes cannot be done properly. Phipps (1979) and Pearlstine et al. (1985) do not consider the fuzziness in the relationships between the abiotic and biotic factors and species growth response – fuzziness in the relationships, due to the difficulty to describe precisely the real system because of its complexity and because of limited quantitative data available (Lexer and Hönninger, 2001). Besides the probabilistic treatment of uncertainty, there are other methods which can be used for treatment of imprecision and heterogeneity, as the application of fuzzy set based methods (Zimmermann, 1996). The application of fuzzy set theory in Gap models has already been demonstrated in by Lexer and Hönninger (2001), who developed a fuzzy logic control unit to model the effect of site nutrient status on vegetation, but also in numerous examples in engineering and decision theory.

In order to use the broad but still vague knowledge about flooding stress response, we present in this paper the application of the fuzzy set theory to flooding stress modelling illustrated for the case of Central European tree species. Flooding stress response to the abiotic factors, duration, depth and frequency of flooding, differs following five flooding tolerance classes defined in Glenz et al. (2005b; Chapter 3) and is expressed by means of a growth factor limiting optimal tree growth (Botkin, 1993; Moore, 1989). The use of flooding tolerance classes allows integrating implicitly the different adaptations (e.g. physiologic, morphologic) to flooding. The flooding tolerance model can be integrated into more complex forest succession models, such as distribution-based or gap models, adapted to riparian areas. Moreover, increasing insights and data about the species-specific processes and tolerances to flooding will allow the 'training' of the fuzzy logic model on quantitative and qualitative data.

A forest succession model including flooding tolerance modelling can present a helpful tool in the decision-making process of large river restoration projects, by illustrating riparian forest dynamics at specific river corridor designs.

## METHOD

The fuzzy set theory allows the use of the broad but still vague knowledge about the complex processes related to flooding stress response. The theory of constructing a fuzzy logic control unit (FLC) was described by Lexer and Hönninger (2001) in their application to model the effect of site nutrient status on vegetation. Fuzzy logic controllers are systems, which use rules instead of algorithms to model knowledge in an explicit manner. Rules link the input variables with the control variable by means of linguistic variables, which can be characterised in a simplified form as a quadruple $(X, T, U, M)$. In it $X$ is the name of the input variable $x$, $T$ denotes the term set of an input variable $x$, and $U$ is the range of the base variable $u$ which is associated with $T(x)$ via the membership function $M$, and $M$ defines the degree of membership of each crisp element of $U$ with respect to $T(x)$. In our application we choose the design generally known as a Mamdani fuzzy controller (Zimmermann, 1996). The input variables are linked with the control variable by rules of the form

$$\text{if } x_1 \text{ is } Q_{1j} \text{ and } x_2 \text{ is } Q_{2j} \text{ and } x_3 \text{ is } Q_{3j} \text{ then } y \text{ is } Q_j,$$

where $Q_{ij}$ is the jth term of a linguistic variable $X_i$ and $Q_j$ is the jth term of the control variable. $x_i$ represent the input variables and y the response variable. A set of rules is constructed for each response category. To parameterise the membership functions $\mu_{ij}(x)$ and $\mu_j(y)$ for each term of the linguistic variables, $x_{max,i}$ and $x_{min,i}$ as well as the range where $\mu_{ij}(x)$ equals one were defined by applying the method of direct rating (Turksen, 1991). The membership grades of all rule antecedents are aggregated to determine the degree of compatibility, $\alpha$, using the minium-operator as a model for the 'and'. The degree of match of each rule is computed as

$$\alpha_r = \min_{i=1,\ldots,n} \left\{ \mu_i^j \left( x_i^{input} \right) \right\}.$$

This concept enables us to obtain the validity of the rule consequences. We assume that rules with low degree of membership in the antecedent also have little validity

and therefore clip the consequence fuzzy sets at the height of the antecedent degree of membership. Formally,

$$\mu_r^{conseq}(y) = \min\{\alpha_r, \mu^i(y)\}.$$

According to Zimmermann (1996) the combined consequences $\mu^{conseq}(y)$ from all rules *(r)* which had 'fired' for a given set of input values were obtained by employing the maximum operator

$$\mu^{conseq}(y) = \max\{\mu_r^{conseq}(y)\} \quad .(1)$$

As we require a crisp control action on a [0, 1]-scale, we selected the centre of gravity method (COG) to generate a crisp value for the control variable. The resulting fuzzy set $\mu^{conseq}(y)$ from Equation (1) is piecewise integrated using a numerical procedure according to

$$y^{COG} = \frac{\sum_{i=1}^{n} \int_{t_i}^{t_{i+1}} y \cdot f(y) \, dx}{\sum_{i=1}^{n} \int_{t_i}^{t_{i+1}} f(y) \, dx}.$$

This approach chooses the control action *(y)* which corresponds to the centre of the area with membership greater than zero weighted with the value of the membership function.

By lack of quantitative data relating shoot growth to responsible abiotic factors, we tested model validity by verifying its conceptual validity according to Rykiel (1996). This includes verification whether the theories and assumptions underlying the model are correct or at least justifiable and that the model's representation of the system, its structure, logic, mathematical and causal relationship is reasonable for its indented use.

# RESULTS AND DISCUSSION

## Application of fuzzy set theory to flooding stress modelling

*Input and control variables*

In our approach, we focus on three abiotic factors (*i.e.* input variables), namely 'flooding depth', 'flooding duration' and 'flooding frequency'. According to Glenz *et al.* (2005a; Chapter 2) the term flooding frequency is replaced by 'time since last flood (TLF)' as the model attempts to simulate the impact of a specific flood on the flooding stress response. Flooding frequency expressing the average number of times a site is flooded for a given time period can be useful if only a rough characterization of the stress due to flooding is required. For sites with floods of short recurrence intervals, flooding frequency may present a good proxy to express this increasing flooding stress. The influence of the aforementioned factors on flooding tolerance has been extensively discussed in Glenz *et al.* (2005a; Chapter 2). Briefly, injury increases as soil saturation progresses, first to partial submersion and then to complete submersion. A species that can survive a certain period of soil saturation or partial submersion will often fail to survive the same period of complete submersion. The reason of the increasing flooding stress from soil submersion to complete submersion is partially due to a reduction of the ability to transport internally and externally oxygen to the roots and out of the roots, consequently affecting plant metabolism. The mechanism that causes increased mortality when crowns are submerged is related to the oxygen deficiency of the submerged aerial tissue during the respiration phase and the reduction of photosynthesis. Concerning 'flooding duration', the longer trees are exposed to flooding, the greater the potential for injury as the decrease in the oxygen supply increasingly affects the trees' biochemical response. Overall, duration of flooding accentuates the effects due to flooding depth. Finally shorter TLF affect development of tree species as the time needed to re-establish the functioning of biochemical processes and to regain vitality after flooding events increases and exposure to post-anoxic stress is accentuated. This may result in a reduced shoot growth or even death. Irrespective of its duration, flooding has little or no effect in the dormant season because of the minimal demand for oxygen by roots and micro-organisms in winter. In this paper we integrate the factor 'Flooding timing' indirectly, as we consider only flooding events within the growing season to affect plant physiology and development.

The input variables 'flooding depth' and 'time since last flood' consisted of three levels; for 'flooding duration' five terms have been defined, as well as for the control

variable 'flooding stress response' or disturbance severity. Consequently the exhaustive state space of the model consists of 45 rules. These 45 rules were defined for each of the five flooding tolerance classes (TCL; very low/TCL 1, low/TCL 2, intermediate/TCL 3, high/TCL 4, very high tolerance/TCL 5) determined for 65 Central European tree and shrub species in Glenz *et al.* (2005b; Chapter 3). The output value based on defuzzification of the control variable 'flooding stress response', corresponds to a flooding growth factor of a specific species, as the most significant and usual symptom of a the lack of oxygen affecting vital physiological functions and metabolic pathways is the decline in shoot growth. A 'severe' flooding stress corresponds to a high impact on optimal tree growth at a specific year resulting in a low flooding growth factor.

*Development of input and control variable membership functions*
The amount of overlap, the width and the shape of different fuzzy sets were defined by expert knowledge integrating also the available quantitative and qualitative data about flooding stress response; see Glenz *et al*. (2005a; Chapter 2). The membership function for 'flooding duration', distinguishes between a 'very short', 'short', 'medium', 'long' and 'very long duration' flood; see Figure 1 (a). Due to the linguistic uncertainty arising from the vagueness in what means a long or a short flood, a higher overlap of the fuzzy sets was considered (Adriaenssens *et al*., 2004). Duration of flooding is considered as the ratio between the number of days within the growing season where soil is submerged by water and the duration of the growing season. For 'flooding depth' a distinction is made between 'shallow' (*i.e.* soil submersion), 'medium' (*i.e.* partial submersion) and 'high' (*i.e.* complete submersion); see Figure 1 (b).
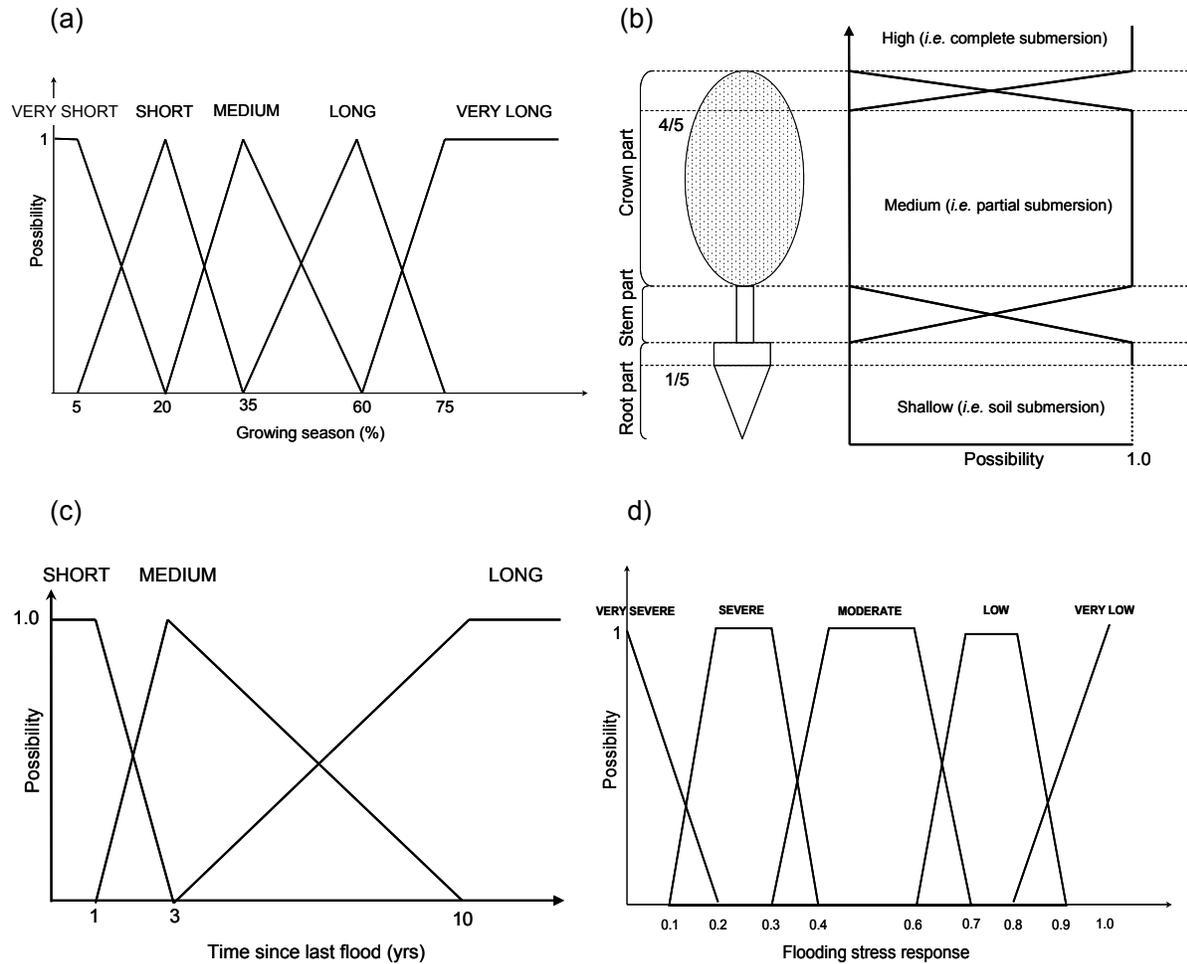
Figure 1: Membership functions for (a) flooding duration (very short, short, medium, long, very long duration), (b) flooding depth (high, medium, shallow flooding depth), (c) time since last flood (short, medium, long time since last flood) and (d) flooding stress response (very severe, severe, moderate, low, very low flooding stress).

As the collected data does usually not allow reconstituting the shape of the flooding wave, the absolute flooding depth corresponds in this case to the maximal flooding depth (m) of a specific flooding event. Soil submersion affecting species development is set at 1/5 of the total rooting depth, as most of the fine roots can be found within the first 20 % of total rooting depth (Kräuchi, 1994). By this, the possibility to model the impact of an increase of the groundwater level on tree and shrub species development is theoretically integrated. Due to the factor 'flooding depth', the effect of submersion will be different following the development stage of tree and shrub individuals or cohorts. The membership function for 'time since last flood' has been separated in 'short', 'medium' and 'long'; see Figure 1 (c). Most of the studies, which

analysed growth response of tree species in respect of flooding, have been made on seedlings under controlled laboratory conditions. It is quite difficult to extrapolate these results to adult trees and to in-situ conditions. Nevertheless, the limits of the control fuzzy set illustrated in Figure 1 (d), have been set with a special regard on studies which addressed the growth response of species under flooded conditions, see for example Ewing, 1996; Gravatt and Kirby, 1998; Kozlowski, 1984; Andersen *et al.,* 1984; Frye and Grosse, 1992; Siebel and Blom, 1998; Siebel *et al.*, 1998. We distinguish between a 'very severe', 'severe', 'moderate, 'low' and a 'very low' flooding stress response (or disturbance severity), with the defuzzified output value 'flooding growth factor' varying between [0,1]. In absence of flooding, the flooding growth factor is equal to one and if the factor falls below a rate of 0.1, flooding conditions are considered to be lethal for shrubs and trees.


*Development of fuzzy rules*

The fuzzy rules relating the abiotic factors to the flooding growth response for each of the five TCL have been developed formulating 'reference points' and interpolating in-between by expert knowledge, integrating the available qualitative (*e.g.* Ehlers, 1960; Goettling, 1968; Moor, 1958; Wendelberger, 1973) and quantitative data of Central European species (*e.g.* Biegelmaier, 2002; Dister, 1983; Gorzelak, 2000; Späth, 1988, 2002; Siebel and Blom, 1998; Siebel *et al.*, 1998). Qualitative indications were for example of the type 'at high floods species *i* is generally completely submerged' or 'species *i* dies in case of long floods' or 'species *i* tolerates soil submersion but less partial submersion'. If possible, these information were completed by quantitative data. For example, based on Biegelmaier (2002), flooding response of adult tree species of different tolerance classes in shallow to medium flooding depths, during a very short flooding period (4-6 days within growing season) were determined. After a depth of 1.30 m and higher, severe effects, even complete mortality for *Prunus avium* (TCL 1) could be observed. *Pinus sylvestris* (TCL 2) showed no effect even until depths of 2.50 m. The indications of Gorzelak (2000) helped to classify species response in the case of a short duration (4 weeks), at low to medium flooding depths and a low flooding frequency. Flood tolerant species as *Salix* spp. and *Populus* spp. presented no signs of damage, whereas *Fagus sylvatica* (TCL 1) died completely, for *Carpinus betulus* (TCL 2) only few species presented damages, similar to the response of *Fraxinus excelsior* (TCL 3). All *Acer pseudoplatanus* trees (TCL 1) died. *Alnus glutinosa* (TCL 5) presented nearly no damage and *Prunus padus* (TCL 4) recovered well in the second year. All individuals of *Larix decidua* (TCL 1) and *Picea abies* (TCL 1) died, but *Pinus sylvestris* (TCL 2) survived and presented quasi no damage signs. The shrub species *Juniperus*

*communis* (TCL 1) also died completely. Complete submergence for a very long flood was considered to be a very sever disturbance even for the most flooding tolerant species. Späth (1988, 2002) determined critical ranges (observed dead trees) of flooding duration for *Salix alba* (TCL 5) at estimated shallow to medium depth floods, of 95% of the growing season. Shorter time spans between flooding events increase disturbance severity and consequently flooding stress response, particularly in the case of short time spans versus medium time spans.

On Figure 2 the developed fuzzy rules, relating specific flooding conditions to the extent of flooding stress (or disturbance severity) for each flooding tolerance class, are schematically represented. Increasing flooding stress, by increasing flooding depths (shallow/soil submersion, S; medium/partial submersion, M; high/complete submersion, H), shorter TLF's (short, medium, long) and duration (very short, VS; short, S; intermediate, M; long, L; very long, VL), affects consequently species development by reducing its growth, resulting in some cases in its death.
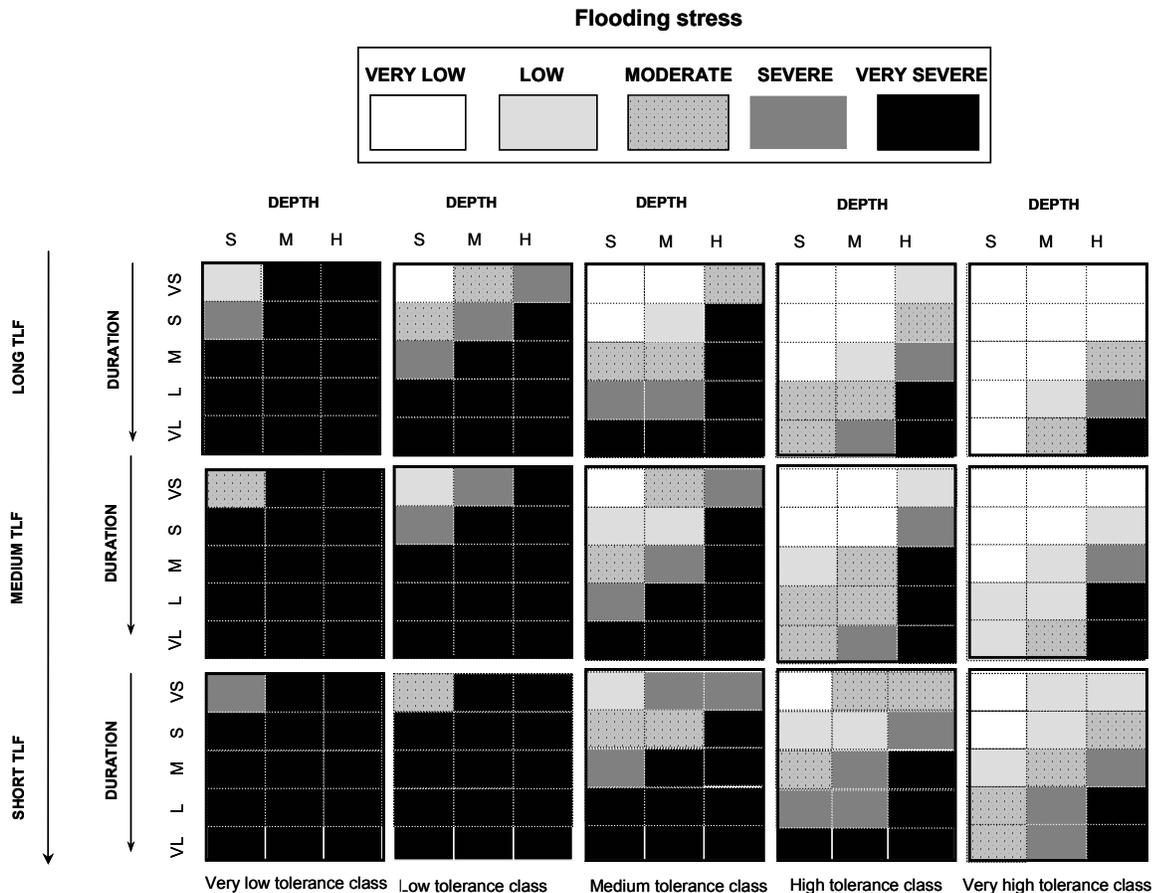
Figure 2: Developed fuzzy rules for the five flooding tolerance classes to model flooding growth stress by increasing flooding depths (shallow/soil submersion, S; medium/partial submersion, M; high/complete submersion, H), TLF's (short, medium, long) and duration (very short, VS; short, S; intermediate, M; long, L; very long, VL).

In the case of a flood of long duration, shallow depth and medium TLF, a species of tolerance class 1 (*e.g. Prunus avium*) would have a very severe response, whereas a species of tolerance class 3 (*e.g. Ulmus minor*) would have a moderate and a species of tolerance class 5 (*e.g. Salix alba*) a very low flooding stress response.

## *Illustration of model behaviour*

The general behaviour of the flooding stress response model is illustrated by two hypothetical examples on data relating vegetation zonation and flooding characteristics for the Rhine river section between Iffezheim and Karlsruhe, Germany. Michiels and Aldinger (2002) gave a general overview of riparian

vegetation zonation related to maximal and mean flooding duration ranges for this Rhine section, as well as maximal flooding depth ranges observed. To simplify, the average values of the flooding duration and depth ranges for each vegetation zone were calculated; see Table 1. The term 'mean flooding conditions' is used to express the measured flooding depths at mean flooding durations, whereas 'maximal flooding conditions' include the same flooding depths but at the maximal measured durations.

Table 1: Riparian vegetation zonation in relation to 'flooding depth' and 'duration', Upper Rhine River, Germany (initially based on Michiels and Aldinger, 2002).

| Vegetation zone | Flooding depth (m) | Flooding duration within growing season | |
| --- | --- | --- | --- |
| | | Maximal duration (days) | Mean duration (days) |
| Low softwood zone | 3.00 | 160.0 | 80.0 |
| Transition soft-hardwood zone | 2.45 | 125.0 | 47.0 |
| Low hardwood zone | 1.95 | 88.0 | 24.0 |
| Medium hardwood zone | 1.30 | 50.0 | 10.0 |
| High hardwood zone | 0.60 | 23.0 | 3.0 |
| Top hardwood zone | 0.15 | 5.0 | 0.5 |

In what follows, two hypothetical examples will be given to demonstrate model behaviour. In the first example we illustrate in more detail the principle of our fuzzy Mamdani-based model, whereas in the second example model behaviour is presented in case of different flooding conditions, with species of different tolerance classes and increasing tree heights.

### *Example 1:*

To illustrate the application of the fuzzy set theory we use following input values: a medium tolerant species (TCL 3), *Ulmus minor*, based on Glenz *et al.* (2005b; Chapter 3), subject to maximal flooding conditions encountered in the low hardwood zone at the river Rhine, see Table 1. TLF is arbitrarily set to 10 years and tree height to 12 m. Stem height is considered to be 1/5 of tree height. The fuzzy Mamdani-based model is displayed in Figure 3. The input values activated four rules out of the state space of 45. The first rule for instance is read as follows: 'if flooding depth is shallow (*i.e.* soil submersion) and flooding duration is medium and time since last

flood is long, then flooding stress response is moderate for a tree of a species $x_1$ (*e.g. Ulmus minor*), with a tree height of $x_2$ (*e.g.* 12 m), a stem height of $x_3$ (*e.g.* 2.4 m) and a flooding tolerance class of $x_4$ (*e.g.* medium flooding tolerance)'.

In Figure 3 a flooding depth of 1.95 m has a membership grade of 0.188 to the fuzzy set 'shallow' (*i.e.* soil submersion) and 0.812 to the fuzzy set 'medium' (*i.e.* partial submersion). A flooding duration of 88 days (= 48.9 % of growing season) has a membership grade of 0.444 to the fuzzy set 'medium' and 0.556 to the fuzzy set 'long' and finally a TLF of 10 years has a membership grade of 1.0 to the fuzzy set 'long'. The membership grades of all three rule antecedents are aggregated to determine the degree of compatibility using the minimum-operator and clip the consequence fuzzy sets at the height of the antecedent degree of membership, *i.e.* for rule (1) at height 0.188. The consequences from rule one to four are then combined by employing the maximum operator. Defuzzification of the fuzzy output by COG results finally in a flooding growth factor of 0.387.

Legend of Figure 3; : Hypothetical example of the fuzzy Mamdani-based model applied to flooding tolerance modelling of tree and shrub species, with the input variables 'flooding depth', 'flooding duration' and TLF and the output value 'flooding growth factor' (*e.g.* 0.387) for the control variable 'flooding stress response' for a tree of species $x_1$ (*e.g. Ulmus minor*), with a tree height of $x_2$ (*e.g.* 12 m), a stem height of $x_3$, (*e.g.* 2.4 m) and a flooding tolerance class of $x_4$ (*e.g.* medium tolerant), after defuzzification with COG of the fuzzy output.
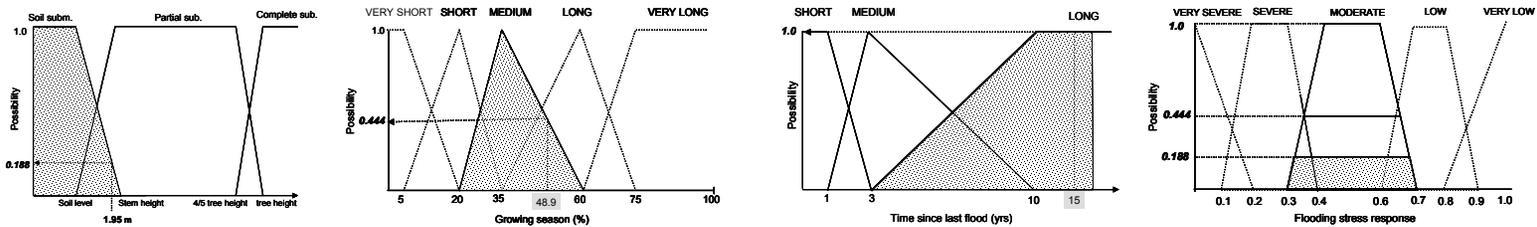
Rule (1): IF flooding depth is **shallow (soil subm.)** and flooding duration is **medium** and time since last flood is **long**, then flooding stress is **moderate** for species $x_1$, at tree height $x_2$, stem height $x_3$ and tolerance class $x_4$.
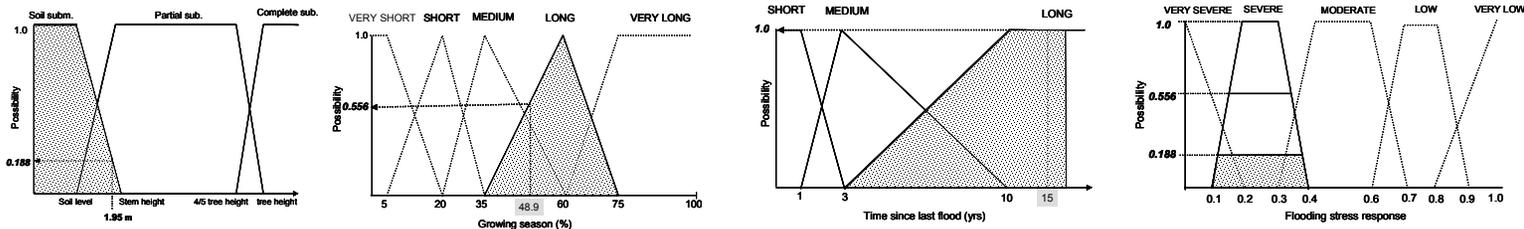


Rule (2): IF flooding depth is **shallow (soil subm.)** and flooding duration is **long** and time since last flood is **long**, then flooding stress is **severe** for species $x_1$, at tree height $x_2$, stem height $x_3$ and tolerance class $x_4$.
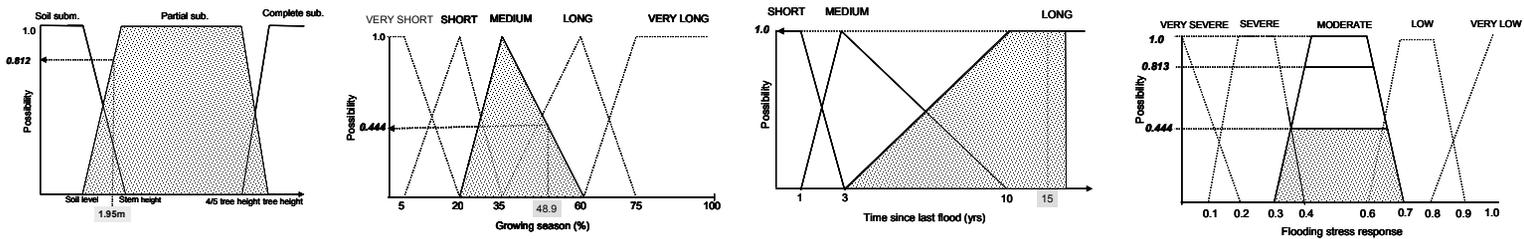


Rule (3): IF flooding depth is **medium (part. subm.)** and flooding duration is **medium** and time since last flood is **long**, then flooding stress is **moderate** for species $x_1$, at tree height $x_2$, stem height $x_3$ and tolerance class $x_4$.



Rule (4): IF flooding depth is **medium (part. subm.)** and flooding duration is **long** and time since last flood is **long**, then flooding stress is **severe** for species $x_1$, at tree height $x_2$, stem height x3 and tolerance class x4.

***Example 2:***

As a second example, model behaviour is presented by applying a flooding stress gradient represented by the mean and maximal flooding co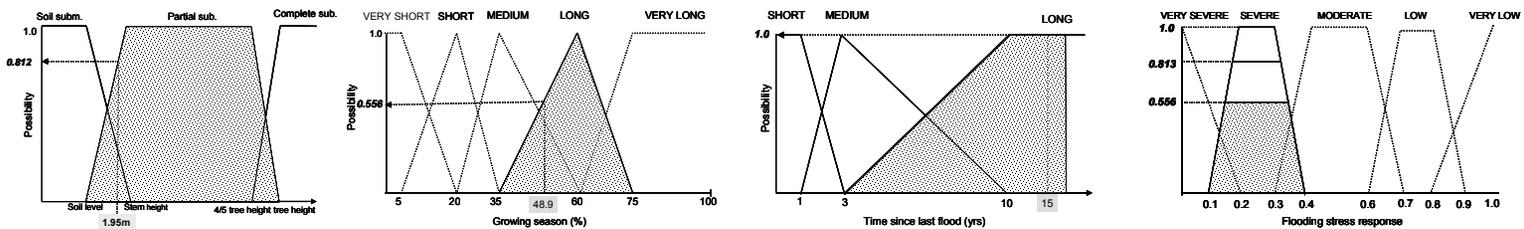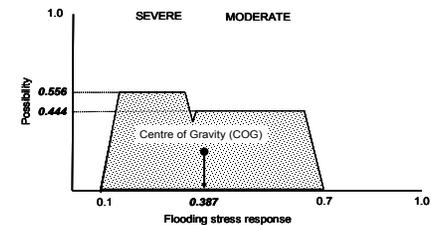nditions observed in the different riparian vegetation zones at the river Rhine (see Table 3), with species of different tolerance classes and tree heights up to 20 m. As in Example 1, TLF is set to 10 years, to allow a better interpretation of the results. Note that the shorter the TLF's, the higher the flooding stress on the considered tree species favouring the more flooding tolerant species. Based on the flooding tolerance classification presented in Glenz *et al.* (2005b; Chapter 3), one typical species of each flooding tolerance class is selected for representation purpose: *Salix alba* representing a very high tolerant species, *Populus nigra* a high tolerant, *Ulmus minor* a medium tolerant, *Carpinus betulus* a low tolerant and *Fagus sylvatica* a very low tolerant species. Their growth responses are modelled using the mean and maximum flooding conditions determined for each vegetation zone. For all species, stem height was fixed at 1/5 of tree height.

On Figure 4 we can see that at increasing tree heights flooding stress reduces and therefore the impact of flooding on tree vitality is reduced too. Particularly small trees are subject to high stress as they are more easily exposed to partial and complete submergence. The response pattern at mean flooding conditions is similar to the one at maximal flooding conditions: However, flooding growth factors are higher allowing lower tolerant species to be viable closer to the river. Even if the presence of the these species at the river Rhine depends not only on flooding tolerance, the result of this static simulation reveals, based on their survival (threshold at a growth factor of 0.1), a species distribution pattern observed at the river Rhine by Michiels and Aldinger (2002), Gerken (1988), Gulder (1996) or Volk (2001). All these authors reported the presence of *Carpinus betulus* and *Fagus sylvatica* mainly in the high to top-hardwood zone, *Ulmus minor* in the low- to medium hard wood zone and *Salix alba* in the softwood zone.
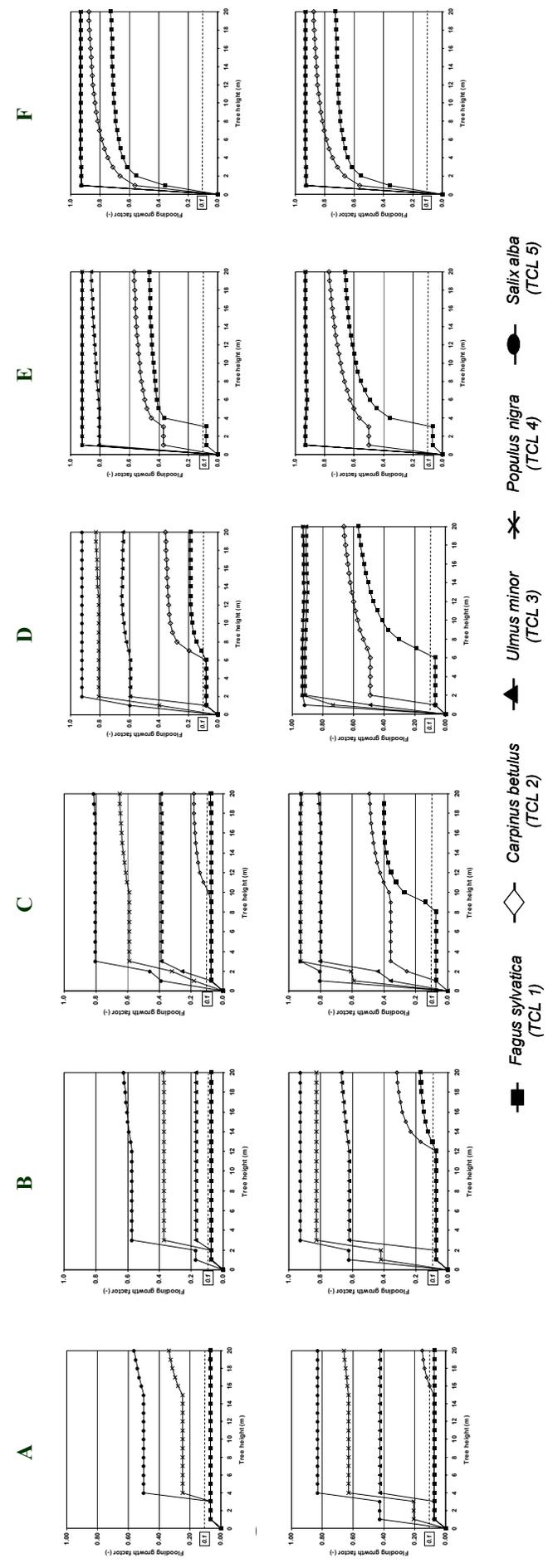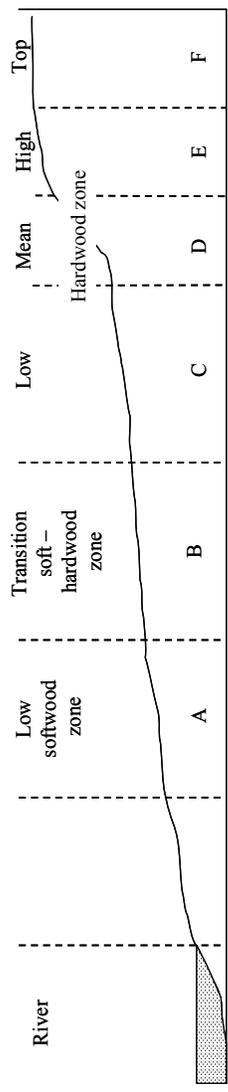
Figure 4: Simulation result of flooding growth response of trees up to 20 m height, at 'maximal' flooding conditions and 'mean' flooding conditions for each vegetation zone.

## CONCLUSION

The developed fuzzy logic system provides a transparent representation of the processes under study and because of this; the system can permanently be updated by new knowledge of qualitative (*e.g.* expert knowledge) or quantitative nature. For instance, once there will be enough experimental field data on flooding stress response of individual tree and shrub species, the possibility of elaborating a 'training set' to reformulate the fuzzy rules (corresponding to the actual state of knowledge) based on exact field-observations, can be considered (Bardossy and Disse, 1993). By this, conceptual validity, which according to Rykiel (1996) can not guarantee for accurate predictions, could be replaced by data validity, increasing model reliability. We consider that the conceptual validity is fulfilled as the use of fuzzy logic is reasonable given the availability and quality of data and as the modelled processes are justified by the actual knowledge about the factors affecting flooding stress response, as reported by Glenz *et al.* (2005a; Chapter 2).
As opposed to non-fuzzy techniques (*e.g.* probabilistic tools), the linguistic uncertainty, implementing the imprecise and vagueness of semantic aspects, as for example the meaning of 'long' or 'shallow' is part of our fuzzy rule based modelling system by the appropriate setting of form and overlap of fuzzy sets. However, one might argue that the construction of membership functions is too subjective; which is indeed a weakness of fuzzy set systems (Adriaenssens *et al*., 2004). On the other hand, the use of membership functions allowed us defining soft thresholds consistent with the ecological knowledge, in contrast to characteristic functions which define hard thresholds in classical set theory.

In summary, forest succession models integrating flooding stress response using fuzzy logic, as well as other ecological, hydraulic and geomorphologic driving-processes specific to riparian areas could present a powerful tool in the decision-making process of restoration projects or retentions basins planning.

## ACKNOWLEDGEMENTS

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# CHAPTER 5

# Quasi-mechanistic vertical root growth model for tree and shrub species

# ABSTRACT

The development of a root system, vertically and horizontally, depends on biotic factors (*e.g.* genetic characteristics, competition) and abiotic factors (*e.g.* soil temperature, soil humidity, light conditions). Up to now, root growth modelling was mostly done for annual plants using logistic and sine root growth functions to simulate 'optimal' root growth affected by changing soil moisture conditions. Concerning trees, only few systematic studies have been done to relate vertical rooting depths of trees to site factors. Moreover, the existing models require data generally not available for a greater set of species. Resulting from the complexity of root dynamics and the lack of systematic quantitative data concerning tree roots and their interaction with environmental factors, a purely mechanistic and individual-based modelling of tree root growth, based on physiologic processes, cannot be done properly. However, vertical root extension modelling would be needed in studies aiming to simulate resistance capacity of tree and shrub species; for example in the case of wind or water flow or in studies interested in a more detailed consideration of the soil water balance in respect of the soil water extraction by roots. In this paper a conceptual based, quasi-mechanistic root growth model for tree and shrub species is presented which considers the genotypical rooting behaviour as well as the effect of abiotic factors (*e.g.* shade and drought) on vertical root extension. The model is conceived for integration into existing forest succession models, which aim to simulate wind or water related disturbances on forest succession, or soil water extraction by roots in view of a more explicit modelling of the soil water balance.

*Keywords: model, root growth, quasi-mechanistic, classification, rooting types, Central Europe*

# INTRODUCTION

The development of a root system, vertically and horizontally, depends on biotic factors (*e.g.* genetic characteristics, competition) and abiotic factors (*e.g.* soil temperature, soil humidity, light conditions, soil compaction and texture, groundwater level or chemical influences); see for example Köstler *et al.* (1968); Lehnardt and Brechtel (1980); Polomski and Kuhn (1998). Up to now, root growth modeling was mostly done for annual plants, like crops (*e.g.* Gerwitz and Page, 1973; Adiku *et al.,* 1996; Chang and Corapcioglu, 1997). Logistic and sine root growth functions have been used, where 'optimal' root growth was affected by changing soil moisture conditions. In opposition to annual plants, perennial plants like trees and shrubs, develop apart from short-living fine roots, responsible for nutrient and water uptake, also long-living structural roots (> 2 mm; Köstler *et al*., 1968), required for tree stability. As vertical structural roots develop from fine roots with vertical orientation, development of structural roots is strongly related to the primary development of fine roots. Concerning trees, only few systematic studies have been done to relate rooting depths of trees to site factors (Polomski and Kuhn, 1998). Most of the root development studies are based on biomass partitioning, trying to determine relationships between above and below-ground biomass (Watson and O'Loughlin, 1990; Enquist and Niklas, 2002; Zens and Webb, 2002). In opposition, Hammel and Kennel (2001) integrated in their soil water balance model, the simulation of vertical and horizontal fine root distribution in relation to stand age. However, this approach needs data, as root density, root length, root growth velocity for the species under consideration – data generally not available for a greater set of species. Most of the quantitative data available for trees and shrub species are punctual observations of rooting depths, mainly of structural roots, in relation to specific soil types and species age (*e.g.* Köstler *et al*., 1968; Stone and Kalisz, 1991; Polomski and Kuhn, 1998).

Regarding the complexity of root dynamics and the lack of systematic quantitative data concerning tree roots and their interaction with environmental factors, a purely mechanistic and individual-based modelling of tree root growth, based on physiologic processes, cannot be done properly. However, the modelling of vertical root extension would be needed in studies aiming to simulate resistance of tree and shrub species to uprooting, as for example in case of wind (Peltola *et al.*, 1999; Gardiner *et al.*, 2000) or water flow, but also in studies interested in a more detailed modelling of the amount of water withdrawn from the pore space by the plants. Forest succession models, distribution-based (Lischke *et al.*, 1998) or gap models (Botkin, 1993), which are all conceived to examine vegetation response to changing environmental

conditions, including disturbances, never treated the aspect of wind load or drag force explicitly. The main reason for this can be found in the complexity of the related physical processes, but also in the lack of data needed for calculating the different forces acting on these trees, *e.g.* crown characteristics and particularly rooting depths of the structural roots at specific development stages. Hence, Kräuchi (1994) considered a species-independent homogenous root distribution to calculate water extraction by roots, ignoring differences of rooting depths between development stages.

In this paper we suggest a conceptual based approach for modelling vertical root growth of tree and shrub species. The genotypical rooting behaviour of Central European tree and shrub species is described by classifying them into rooting types, for whom the generally observed vertical extension and temporal growth pattern were determined. Finally, we suggest a quasi-mechanistic vertical root growth model by considering the abiotic factors affecting vertical root extension. The model is conceived for integration into existing forest succession models, which aim to simulate wind or water related disturbances on forest succession, or soil water extraction by roots in view of a more explicit modelling of the soil water balance.

## MODEL FRAMEWORK

The development of a root system depends primarily on species-specific genetic characteristics, but also on environmental conditions as well as on inter-specific competition for space and consequently resources. Based on Kraus (1914), Köstler *et al.* (1968), Gale and Grigal (1987), we suppose that under 'favourable' (*i.e.* no physical or physiological limitations) site conditions root extension is determined by the genetic constitution of each species. According to Köstler *et al.* (1968) soil conditions, required for an uninhibited ('optimal') root growth, can be specified by a high porosity, homogenous soil moisture and aeration conditions. We characterize genotypical rooting behaviour of the structural roots by the maximal rooting depths reached and the temporal root growth pattern. An overview of the modelling framework is given in Figure 1.
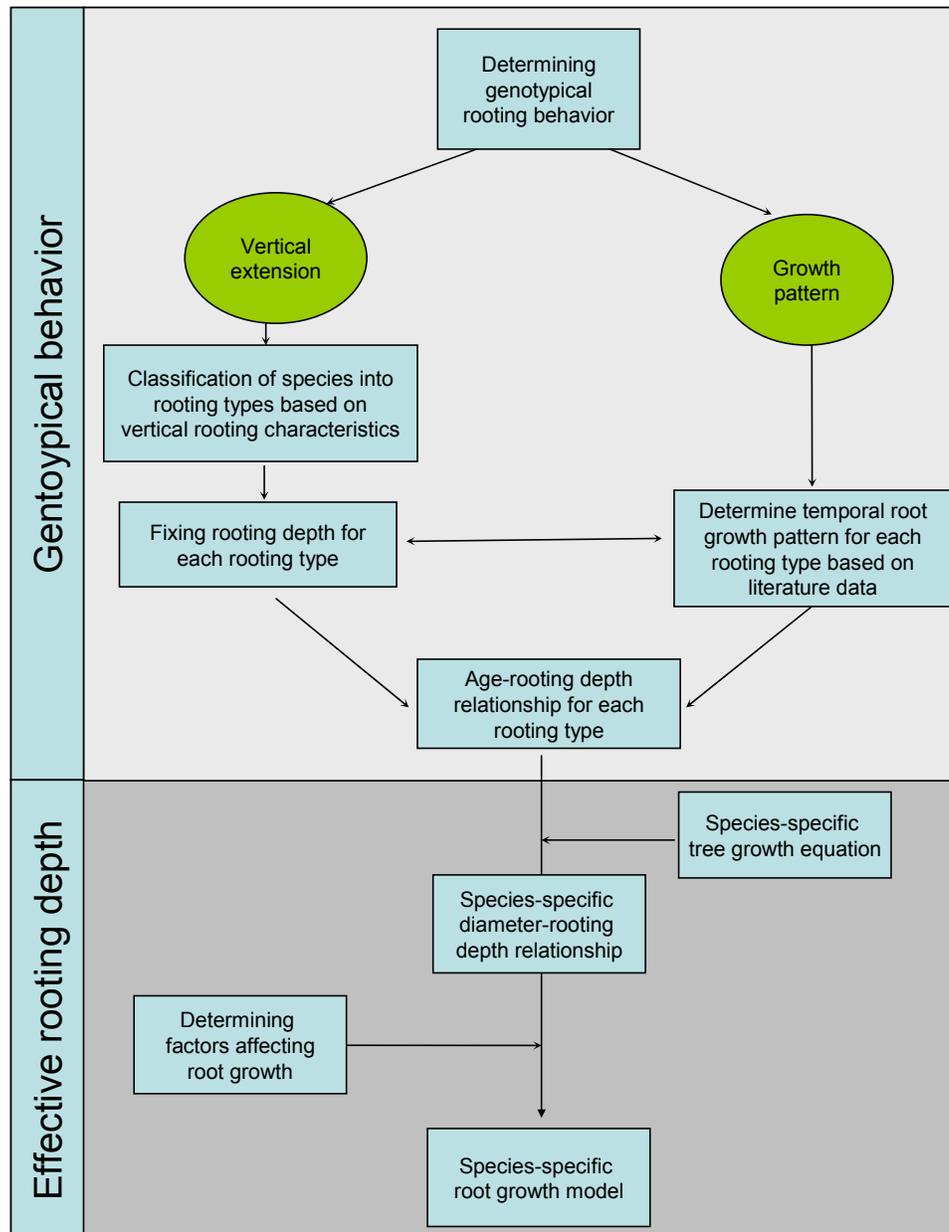
Figure 1: Overview of the model framework of the vertical root growth model.

## Classification into rooting types

Available information about species-specific maximum rooting depths of trees and shrubs differ (*e.g.* Köstler *et al*., 1968; Stone and Kalisz, 1991; Polomski and Kuhn, 1998), depending on the environmental conditions found on the respective study sites. The lack of species-specific quantitative data of maximal root extensions at 'favourable' site conditions requires a classification based on the general observed

rooting growth pattern of each tree and shrub species. Hereafter we assume that this is the genotypical rooting pattern. Although root system architecture results of the interaction of the root system with several environmental factors, the possibility to classify tree root systems has also been pointed out by Drexhage *et al.* (1999).

Kreutzer (1961) analyzed rooting depth on pseudogley soils and separated tree species rooting types in a shallow rooting group (<60 cm), for *Sorbus aucuparia*, an intermediate rooting group (60-120 cm), for *Larix decidua*, *Carpinus betulus*, *Fagus sylvatica* and *Alnus incana* and a deep rooting group (>120 cm) for *Quercus robur, Quercus petraea, Alnus glutinosa* and *Populus tremula*. In addition, Polomski and Kuhn (1998) made a classification of the vertical root extension of Central European tree and shrub species, based on their morphological characteristics. The authors differentiated between very shallow rooters (<20 cm), shallow rooters (20-40 cm), intermediate rooters (40-80 cm), deep rooters (80-130 cm) and very deep rooters (> 130 cm), based on the classification of Blume (1991). We assume that this classification represents the genetically determined vertical rooting behavior. Based on the indications of Kreutzer (1961), Köstler *et al.* (1968), Polomski and Kuhn (1998) and Kutschera and Lichtenegger (2002), a classification of tree and shrub species in three rooting types is performed: 'rooting type (RT) 1' corresponding to more shallow rooting species, 'RT 2' to intermediate rooting species and 'RT 3' to deep rooting species. A classification into three rooting types was estimated to be reasonable in regard of the data available and the model's indented use. Tree and shrub species classified by Polomski and Kuhn (1998) as intermediate or as deep rooters, were associated to RT 2. Following Kreutzer (1961) and Polomski and Kuhn (1998), the maximum rooting depth of RT 1 was set to 60 cm, 130 cm for RT 2 and arbitrarily 200 cm for RT 3. However, for all the three rooting types, maximal rooting depth is constraint by the soil depth or by the permanent groundwater level.

## Determination of vertical root growth pattern

Coile (1937) noted that root density increases with age, however horizontal and vertical extent of roots is reached at a certain age. Polomski and Kuhn (2001) described four root system development stages, indicating that timing and duration of these stages are influenced by genetic as well as site-specific factors. The first 2 to 3 years can be noted as 'tap-root phase', dominated by an intensive vertical root growth (stage 1). During the next 10 years a 'differentiation' of root types (vertical, horizontal *etc.*) can be observed. The authors claim that a lot of trees have at this stage already a well-developed tap-root, reaching nearly maximum depth (stage 2). A number of trees, such as *Abies alba, Picea abies, Pinus sylvestris* or *Quercus* spp. develop between 10 to 30 years, the so-called sinker roots. The vertical growth of

roots is reduced but the horizontal development continues. The definitive (*i.e.* maximum) rooting depth is reached after about 40 years (stage 3). Finally, stage 4 is typical for death of root parts and complementary development of new parts. Nörr *et al.* (2002) based their analysis of root development also on the development stages cited in Polomski and Kuhn (2001). In opposition, Lehnardt and Brechtel (1980), which analyzed rooting depths at forest stands of different species and age classes are claiming that maximum rooting depth is reached for the most of the species after 60-80 years. However, Mitscherlich (1978) mentioned that complete horizontal and vertical extension is reached at an early stage of tree development, namely after 20 to 40 years – being in accordance to Polomksi and Kuhn (2001). Following Kalela (1954) the root system of *Pinus sylvestris* is completed after 35-40 years. Based on these studies we suppose that the maximal vertical rooting depth is reached at age 35 to 40.

To determine the temporal pattern of the age-rooting depth relationship for each rooting type (*e.g.* logistic, quadratic or exponential) and to validate the assumptions made, some species-specific observations on trees relating rooting depth to species age have been collected in the literature (*e.g.* Hoffmann, 1966; Köstler *et al.*, 1968; Lehnardt and Brechtel, 1980; Polomski and Kuhn, 1998; Raissi *et al.*, 2001); for *Abies alba* 3 observations on individuals, for *Fagus sylvatica* 12, for *Quercus* spp. 11, for *Larix decidua* and *Acer pseudoplatanus* 10, for *Alnus glutinosa* 7, for *Robinia pseudo-acacia* 2, for *Populus nigra* 9, for *Picea abies* 6, for *Fraxinus excelsior* 2, for *Betula pendula* and *Carpinus betulus* 4, for *Malus sylvestris* 1 and for *Tilia cordata* 2. As the rooting pattern of the species within the same rooting type class is supposed to be equal, the individual observations have been regrouped following the rooting type classification of the corresponding tree and shrub species. Note that mainly data of soil types have been considered, which assert an uninhibited root development, such as deep, loamy sandy soils (Köstler *et al.*, 1968). Observations for which it was obvious that root growth was severely limited by abiotic barriers (*e.g.* soil depth, groundwater) were ignored. Moreover, we suppose that except of the two cited barriers, no other abiotic root growth restrictions exist, as only under these considerations a clear relationship between root growth and age can be observed; see Polomksi and Kuhn (1998) for *Pinus sylvestris*.


## Factors affecting root growth

In most cases, site conditions are not optimal for root development and abiotic factors (*e.g.* soil temperature, soil humidity, light conditions, soil compaction and texture) or biotic factors (*e.g.* competition) affect vertical root extension, either

positively by enhancing or negatively by inhibiting root growth. In general, the more a plant species is driven to the limits of its ecological amplitude, the more its initial genetically determined rooting pattern is affected.

According to Polomski and Kuhn (2001), the effect of light is particularly important for young trees. Reduced light availability increases the 'shoot/root' ratio (Mitscherlich, 1978) as carbon resources are used for shoot development (Kutschera and Lichtenegger, 2002) and consequently no exceed of photosynthesis assimilates can be stocked in the roots. To note that in conditions of shading, the reduction of root growth is not only the result of a reduced production and storing of photosynthesis assimilates, but also of a reduced soil temperature.

Concerning root growth response to drought, two situations have to be considered, namely the presence or absence of a hydrotropic stimulus, which means the attraction of roots by distant water sources (*e.g.* presence of groundwater). Hence, in case of drought, an enhanced vertical root growth can only be observed where roots receive a hydrotropic stimulus of deeper soil parts (Köstler *et al.*, 1968), as for example in floodplains due to shallower groundwater levels (Hughes *et al.*, 1997). In the absence of a hydrotropic stimulus, vertical root extension is reduced.

Maximal vertical extension is physically limited by soil depth (Köstler *et al.*, 1968; Hainard *et al.*, 1987) and physiologically by a permanent groundwater level as roots of the most of the tree and shrub species do not tolerate anoxic conditions (Köstler *et al.*, 1968; Wendelberger, 1973; Mitscherlich, 1978; Lehnardt and Brechtel, 1980; Hainard *et al.*, 1987; Polomski and Kuhn, 2001). Even deep rooting species develop a shallow root system at a permanent high groundwater level. However, *Quercus robur, Pinus sylvestris* and *Alnus glutinosa* may present exceptions, as roots of these species can penetrate the groundwater zone (Lehnardt and Brechtel, 1980).

In what follows, we suppose that apart from the physical and physiological limits (*e.g.* soil depth, groundwater level), mainly soil moisture conditions (Köstler *et al.*, 1968) and, to a fewer extent, light availability affect vertical root development.

# MODEL DEVELOPMENT

In what follows the results of the rooting type classification and the determination of the vertical root growth pattern are listed, together with vertical root growth model development.

Table 1 shows the classification of 65 Central European tree and shrub species into three rooting types representing their genotypical rooting characteristic.

Table 1: Classification of 65 Central European tree and shrub
species into rooting types (RT).

| RT 1 | RT 2 | | RT 3 | |
|---|---|---|---|---|
| *Alnus viridis* | *Acer campestre* | *Alnus incana* | *Pinus silvestris* | *Salix m. nigricans* |
| *Cornus sanguinea* | *Aesculus hipp.* | *Acer platanoides* | *Quercus petraea* | *Salix pentandra* |
| *Frangula alnus* | *Betula pendula* | *Amelancier ovalis* | *Quercus pubescens* | *Salix purpurea* |
| *Ilex aquifolium* | *Fraxinus excelsior* | *Populus alba* | *Quercus robur* | *Salix triandra* |
| *Ligustrum vulgare* | *Prunus spinosa* | *Castanae sativa* | *Robinia pseudo.* | *Salix viminalis* |
| *Lonicera xylosteum* | *Prunus domestica* | *Corylus avellana* | *Salix alba* | *Acer pseudopl.* |
| *Prunus avium* | *Prunus padus* | *Crataegus laevigata* | *Salix appendiculata* | *Alnus glutinosa* |
| *Rhamnus cathartica* | *Prunus mahaleb* | *Crat. monogyna* | *Salix caprea* | *Ulmus minor* |
| *Viburnum opulus* | *Sorbus aucuparia* | *Hipp. rhamnoides* | *Salix cinerea* | *Larix decidua* |
| *Sambucus nigra* | *Ulmus glabra* | *Juglans regia* | *Salix daphnoides* | *Populus nigra* |
| *Picea abies* | *Abies alba* | *Juniperus com.* | *Salix elaeagnos* | *Fagus sylvatica* |
| | *Tilia platyphyllos* | *Sorbus aria* | *Salix fragilis* | |
| | *Viburnum lantana* | *Taxus baccata* | | |
| | *Cornus mas* | *Tilia cordata* | | |
| | *Carpinus betulus* | *Malus sylvestris* | | |
| | *Populus tremula* | | | |

In all, 11 species were classed as RT 1, 31 species as RT 2, and 23 species as RT 3. Species of RT 3, representing very deep rooting species, are mainly shade intolerant species, such as *Salix* spp. and *Populus* spp.; being in accordance with the observations of Gale and Grigal (1987). Based on the collected literature data revealing very deep vertical extensions for *Larix decidua* and *Fagus sylvatica,* these two species were considered as deep rooting species, in opposition to the initial classification of Polomski and Kuhn (1998). Note that every classification is only as good as the information about the classified objects is, and that a classification remains still a simplification of a considered system. In this sense, the main aim of this classification is to catch the general behaviour of vertical rooting of tree and shrub species in the case of limited data availability.

In Figure 2 the species-specific rooting depth observations found in the literature, regrouped by the three rooting types, are displayed in relation to age. One notices an enhanced root growth in the first years, followed by an exponential relationship of vertical root depth extension with species age. This relationship can be formulated by

$$RD_t = RD_{\max,RT} \cdot \left\{1 - \exp\left(b \cdot A\right)\right\}, \quad (1)$$

where $RD_t$ is the rooting depth at time $t$ (cm), $RD_{max,RT}$ the maximal rooting depth (cm) of the corresponding rooting type ($RT$), $A$ denotes the age of an individual tree or shrub of species $s$ (yrs) and $b$ is a negative non-linear regression coefficient.

Determination of the 'theoretical models' for the three rooting types based on Equation (1) was based on the assumptions that, first, RT 1 has a $RD_{max}$ of 60 cm, RT 2 of 130 cm and RT 3 of 200 cm, and second that 95 % of $RD_{max}$ is reached at age 35 under optimal conditions. The resulting theoretical models with a calculated regression coefficient $b$ = - 0.086 are displayed in Figure 2.
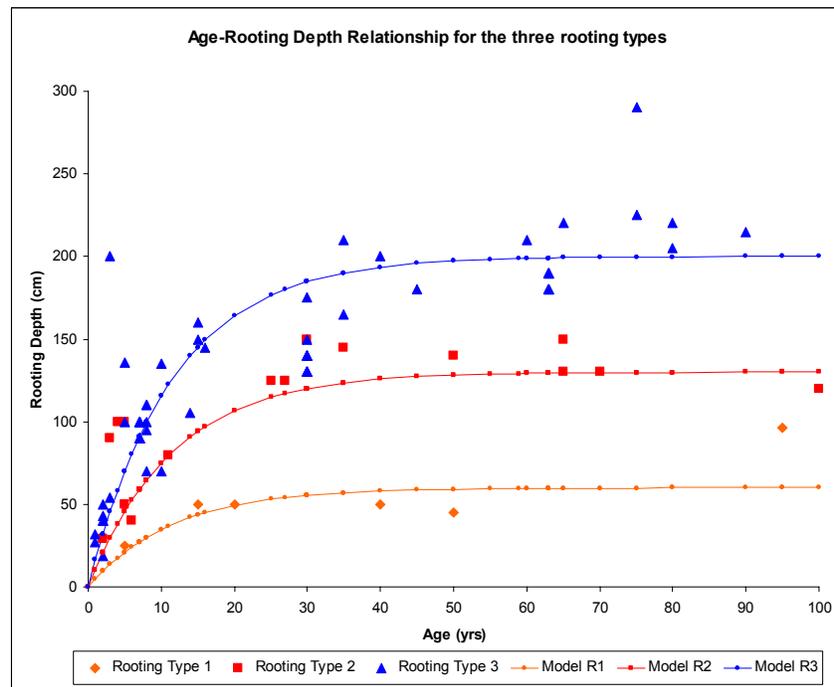


Figure 2: Age-rooting depth relationship for the three rooting types based on the regrouped species-specific data (obtained from the literature) with the corresponding 'theoretical' models.

Apart the fact that based on the aggregated punctual observations, one could conclude that there exists an exponential relationship between 'Age' and 'Rooting depth', a partial validation of the previous assumptions can also be made. First, all three rooting types reach a maximum rooting depth after about 30-45 years, as already pointed out by Coile (1937), Kalela (1954), Lehnardt and Brechtel (1980) and Polomski and Kuhn (2001). Second, the fixed maximal rooting depths for each rooting type correspond more or less to the maximal rooting depths of the observational data. However, as still outlying values can be determined, the exponential fit with fixed maximal rooting depths is only partially satisfactory. This may due to particular site conditions causing a shallower or a deeper rooting. A separate estimation of the non-linear regression coefficients for each rooting type was not investigated as (a), not enough data for shallow and intermediate rooting species were available and (b), more detailed knowledge about the punctual observations, particularly the corresponding soil types, would be needed in order to eliminate misleading 'non optimal' conditions and the associated rooting depths.

## Vertical root growth model

Based on the tree growth equation of forest succession models (*e.g.* Moore, 1989), calculating yearly diameter increment at breast height, and assuming a linear age-diameter relationship up to an age of 40 years (Bugmann, 1994; Figure 3.6), the age-rooting depth relationship (Equation 1) is transformed into an allometric diameter-rooting depth relationship for each species *s* given by

$$ RD_s = RD_{max,RT} \cdot \left\{ 1 - \exp\left( c_s \cdot DBH_s \right) \right\}, $$

where $RD_s$ is the actual rooting depth for species *s* (cm), $RD_{max,RT}$ the maximal rooting depth of rooting type $RT$ (cm), $DBH_s$ denotes the actual diameter at breast height (cm) for a tree or shrub of species *s*, $c_s$ the necessary species-specific regression coefficient (< 0) calculated by

$$ c_s = DBH_{s,t}^{-1} \cdot \ln \left\{ 1 - \left( RD_{s,t} \cdot RD_{max,RT}^{-1} \right) \right\}, $$

where $RD_{s,t}$ is the rooting depth (cm) at time *t* (yrs), $RD_{max,RT}$ the maximal rooting depth of rooting type $RT$ (cm), and finally $DBH_{s,t}$ the diameter at breast height (cm) at time *t* (yrs).

The transformation into a diameter-rooting depth relationship is required as (a) dendrometric relationships are often related to diameter at breast height; (b) it allows illustrating shoot development simultaneously with root development, and (c) many forest succession models do not handle species age as a state variable (*e.g.* TreeMig, Lischke *et al.*, 2005).

As the diameter-age relationship is different for each species, every tree and shrub species within a same rooting type class has a different rooting depth-diameter relationship.

Based on the allometric diameter–rooting depth relationship, a vertical root growth equation is formulated to more dynamically model root growth of each species accounting for environmental stresses ($E_F$), such as shade and drought, affecting vertical root extension. Formally the root growth model for a species $s$ at a yearly diameter increment $dDBH_s$ is given by,

$$\frac{dRD_s}{dDBH_s} = -RD_{max,RT} \cdot E_{F,s} \cdot c_s \cdot \exp\left(c_s \cdot DBH_s\right),$$

where $dRD_s$ is the root depth increment (cm), $dDBH_s$ is the diameter increment at breast height (cm), $RD_{max,RT}$ the maximum rooting depth for each rooting type $RT$ (cm), $DBH_s$ the actual diameter at breast height (cm), $E_{F,s}$ denotes the environmental stress and $c_s$ as mentioned before.

As seen, the formulated root growth model integrates environmental stress factors, such as drought and shading. Most of the existing forest succession models, *e.g.* FORSUM (Kräuchi, 1994), FORCLIM (Bugmann, 1994), TreeMig (Lischke *et al.*, 2005), consider already the effect of environmental stress on shoot growth by use of growth factors (scaled between 0 and 1), and hence affecting optimal tree growth. A growth factor of 1 does not affect optimal shoot growth, whereas lower values express conditions of stress reducing consequently optimal growth. Differences in species sensibility towards these environmental stresses are considered by a previous classification of species into tolerance classes. In this sense, 'growth factors' express the stress affecting shoot development, what consequently influences root development. Based on the previous argumentation, if shoot parts are stressed by a lower light growth factor (LGF), root growth will be also reduced. On

the other hand, if shoot parts are stressed – in the case of a drought – by a low soil moisture growth factor (SMGF), root growth is enhanced in order to reach deeper moist soil parts, but only in the presence of a hydrotropic stimulus. In absence of this stimulus, vertical root extension would be reduced.

In presence of a hydrotropic stimulus (*e.g.* case of shallow groundwater levels), we suggest the following formulation of $E_F$ for a species $s$,

$$E_{F,s} = \left\{ Max_R - \left( Max_R - 1 \right) \cdot SMGF_s \right\} \cdot \sqrt[3]{LGF_s}$$

whereas in absence of such as stimulus we have,

$$E_{F,s} = SMGF_s \cdot \sqrt[3]{LGF_s} \ ,$$

where $E_{F,s}$ represents the environmental stress, $LGF_s$ the light growth factor of the shoot part, $SMGF_s$ denotes the soil moisture growth factor of the shoot part and $Max_R$, the maximal possible increment rate in presence of a hydrotropic stimulus. $Max_R$ is set to 4 following maximal rooting depth ranges of the considered rooting types. Vertical extension is constraint by the permanent groundwater level or soil depth.

## MODEL APPLICATION

To illustrate the behaviour of the described model we select three tree species – one for each rooting type: *Picea abies*, *Fagus sylvatica* and *Alnus glutinosa*. The species-specific characteristics required by the tree growth equation of Moore (1989) to simulate shoot growth similarly with vertical root growth are listed in Table 2.

Table 2: Tree characteristics for vertical root growth modeling (following Bugmann, 1994).
$D_{max}$: Maximal diameter at breast height (cm), $H_{max}$ : Maximal height (m),
G: Constant growth parameter (cm/yr) .

| Species | RT | $D_{max}$ (cm) | $H_{max}$ (m) | G (cm/yr) |
|---|---|---|---|---|
| *Picea abies* | 1 | 210 | 58 | 171 |
| *Fagus sylvatica* | 2 | 225 | 45 | 191 |
| *Alnus glutinosa* | 3 | 130 | 31 | 250 |

The shoot and root parts of every species are subjected to stress conditions of increasing severity by varying the values of the environmental factors at different periods of time: 'low stress conditions' (*SMGF* = 0.8, *LGF* = 0.8); 'medium stress conditions' (*SMGF* = 0.5, *LGF* = 0.5); 'high stress conditions' (*SMGF* = 0.2; *LGF* = 0.2). We consider a scenario in which a period of drought persists from age 3 to 5 and from 11 to 15, and a persisting shading stress after age 18. Soil depth is fixed at 3.00 m and the groundwater level at 2.50 m. Simulations of vertical root growth are done in presence and absence of a hydrotropic stimulus and the results are then presented as diameter-rooting depth relationships. The described simulations were simultaneously run for the shoot and root parts for 50 years. Figure 3 displays the simulation result for the three rooting types at increasing environmental stress levels. The 'No.Stress' curve represents root growth without environmental disturbances – neither inhibiting nor enhancing growth. The other growth curves represent the vertical root growth at the three different stress levels, in presence (*e.g.* 'Low.Stress.Hydro') or in absence (*e.g.* 'Low.Stress') of a hydrotropic stimulus. The differences in curve lengths are due to the fact that increased environmental stress levels reduce also tree diameter increment. Hence, after 50 years of simulation, the more stressed individuals have a smaller diameter at breast height than the others of the same species.
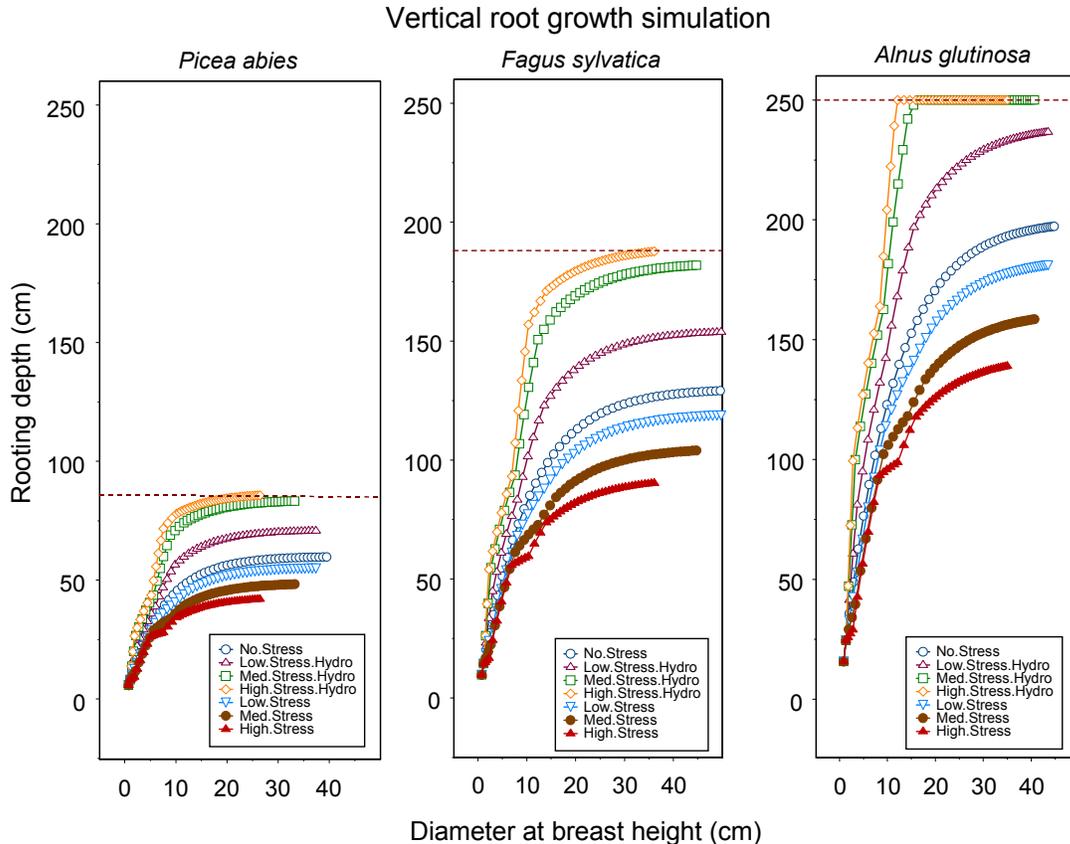
Figure 3: Simulation result of vertical root growth for *Picea abies*, *Fagus sylvatica* and *Alnus glutinosa* at different environmental stress levels. Maximal depths reached indicated with dashed lines.

In the case of a hydrotropic stimulus, an increasing drought stress entails a deeper rooting, as it can be observed for each tree species. At maximal stress conditions, *Picea abies* reaches a rooting depth of 85 cm, *Fagus sylvatica* of 187 cm and *Alnus glutinosa* of 250 cm – the groundwater level; see dashed lines of Figure 3. Taking into account that *Alnus glutinosa* is adapted to tolerate temporarily anoxic conditions, one may assume that root growth continues within the groundwater zone which would result in maximal rooting depth of 494 cm. In opposition, on sites without hydrotropic stimulus, shade and drought are reducing vertical root growth, limiting vertical extension of *Alnus glutinosa* to 139 cm after 50 years. Following Figure 3 one recognizes that despite the so-called genotypical rooting patterns (*i.e.* curves without stress), the rooting behaviour is changing following the severity of the environmental stress conditions affecting shoot growth. The effects are even stronger the earlier they happen in respect of the development stage of an individual as potential relative rooting depth increment decreases with increasing diameter at breast height. But,

only as long as they do not kill the trees or shrubs in consideration. Note that species differ in their tolerance of environmental stress conditions. Hence, similar site conditions will affect vertical rooting growth response differently in respect of the species stress tolerance.

For all three tree species, rooting depths can be found in the literature, corresponding to the simulated ones. However, they can not be accounted for a data validation as they are mainly punctual observations, whereas a continuous record of the environmental conditions during vertical root growth would be required. Nevertheless, the conceptual development of the model is based on the actual knowledge about the rooting behaviour of tree and shrub species under different environmental conditions. Furthermore the model is reproducing plausibly observed ecological behaviour in a justifiable manner for its intended use.

# CONCLUSION

Root growth is complex and depends on a multitude of biotic and abiotic factors. Due to the lack of systematic quantitative data we proposed herein a quasi-mechanistic model to simulate vertical root growth of tree and shrub species – a model which can easily be integrated into existing forest succession models. Based on three described genotypical rooting types, the model integrates the ability to adapt vertical rooting behaviour following changing environmental conditions, either by enhancing or by inhibiting root growth. This by influencing optimal root growth rates by environmental stress factors, as drought stress or shading. Combined with the estimation of the horizontal extension of roots and the geometrical rooting form, uprooting resistance of trees and shrub species to wind or water flow can be calculated by existing mechanistic models (Gardiner *et al.*, 2000; Peltola *et al.,* 1999). Apart from mechanical aspects, the vertical root growth model allows, combined with a depth-depended root distribution function (*e.g.* FORSUM, Kräuchi, 1994), calculating more accurately root extraction rates (*i.e.* transpiration), and consequently the soil water balance or drought stress of individual tree and shrub species. Drought stress of plants occurs in situations where actual transpiration is less than potential transpiration, therefore the ratio of actual transpiration and potential transpiration is used as indicator for drought stress (*e.g.* Pastor and Post, 1985; Kienast, 1987; Bugmann, 1994). Moreover, a vertical root growth model allows simulating the ability of trees or shrubs to reach the groundwater level excluding them from drought stress – a process important in riparian areas. In this sense, the quality of calculating drought stress of individual trees/shrubs or tree/shrub cohorts could be improved by

integrating a vertical root growth model. However, the model can steadily be improved at several levels: (a) at the rooting type classification level by reclassifying species after new insights; (b) by formulating supplementary physiological or physical stress factors (*e.g.* mechanical resistance, influence of temperature, lack of oxygen) and (c) the consideration of dying root parts. Vertical root growth behavior changes following the mechanical resistance encountered in the different soil horizons, affecting by this root penetration ability. Such supplementary stress factors can be added to the model case by case. This is already done in existing forest succession models for modeling shoot growth. For example mechanical resistance could be characterized by soil porosity and soil texture (Köstler *et al.,* 1968) and species-specific differences in mechanical stress sensibility by classifying the species into tolerance classes.

Due to the lack of data concerning the relationship of vertical root growth rates and the affecting abiotic or biotic stress factors, theoretical model validity can only be verified by its conceptual validity. According to Rykiel (1996) conceptual validity means that theories and assumptions underlying the model are correct or at least justifiable and that the models representation of the problem or system is reasonable for the model's indented use. It includes also the justification of using simplifications of known processes and for conjectured relationships of poorly known processes and mechanisms. Based on the argumentation on which the modelling framework is based on we consider the conceptual validity fulfilled. However, data validation and calibration of the model by systematic studies are still required and would increase reliability of the model. Once quantitative data of optimal temporal rooting growth patterns and reached maximum depths for a larger set of species are available, the step from the theoretical modelling approach to the empirical based modelling approach can be done.

# ACKNOWLEDGEGMENTS

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# CHAPTER 6

# RIFOD – A spatially-explicit riparian forest dynamics model

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# ABSTRACT

During the last decades public awareness of the limitations of traditional engineering practices and the imperative to conserve nature have led to changes in river management; including river restoration measures. The enlargement of the fluvial corridor is one of the often considered management measures. However, the high-pressure on land-use, the conflict of interests, as well as the uncertainty of vegetation and landscape development scenarios after restoration, can make their implementation difficult. Herein we present a coupled model of ecological and hydraulic processes to simulate riparian forest dynamics for Central European conditions, particularly for the case of enlarged fluvial corridors. The developed model RIFOD ('RIparian FOrest Dynamics') – a distribution-based forest succession model coupled to a quasi-2D hydraulic model – simulates short or long-term riparian forest dynamics at a yearly time step. The model, applied on a 10 times 10 m mesh grid, is spatially-explicit concerning the interactions of the ecological and hydraulic processes and integrates 65 Central European tree and shrub species. RIFOD is the first process-based spatially explicit riparian forest dynamics model for Central Europe and is based on developments of existing upland forest succession models, which at the process level were improved, adapted and completed according to the ecological gradients observed in riparian areas (*e.g.* flooding, nutrients, moisture). The model finds its application in riparian areas in which the geomorphological activity of the river is not a dominant process or in case of restoration projects, for widened fluvial corridors with geomorphologically stable stream channels. The model is evaluated and applied at different fluvial corridor designs of the River Rhone (Switzerland) in order to illustrate the ecological consequences of a restoration variant for woody vegetation, and to discuss current scientific concepts and hypotheses of riparian ecosystems. Simulation of riparian forest dynamics under different hydraulic conditions can be a helpful tool in the decision-making process of large river restoration projects (or the planning of retention basins), for instance by opposing their ecological gain to the land used. Moreover, it allows a better understanding of the riparian system and its driving-processes.

*Keywords; RIFOD, modelling, forest dynamics, restoration, riparian system, Central Europe*

# INTRODUCTION

Extensive efforts have been made in recent years to restore rivers and their systems with a view to increase the ecological value of riparian areas and the surrounding landscape and to improve the protection provided against extreme flooding events (Buijse *et al.*, 2002). Fluvial corridor enlargement, *i.e.* the enlargement of the section between the levees with the aim of re-establishing quasi-natural river dynamics and the associated typical riparian vegetation, is a often applied restoration measure (Habersack *et al.,* 2000). Width of the fluvial corridor (*i.e.* the area allocated mainly to flood protection) is an important design parameter affecting, in relation to the hydraulic and geomorphologic conditions, potentiality for a successful establishment of woody vegetation. On the other hand, as often, the high pressure on land use of river adjacent areas may bring along a controversial debate making public acceptance and realization of restoration projects difficult. In actual decision-making processes of large river restoration projects, no dynamic long-term modelling approach of potential riparian woody species development exists considering also hydraulic and geomorphological processes. This can be attributed to the complexity of interacting driving-processes (*e.g.* ecological, hydraulic, geomorphological processes) – creating longitudinal gradients at a large and typically sharp lateral gradients at a small scale (Gregory *et al.*, 1991) affecting typical riparian vegetation distribution (zonation). However, models can help to integrate current knowledge, to analyse observations, to test scenarios of different constellations and consequently increase the understanding of complex systems and their interactions, including riparian systems. At the basis of riparian woody species dynamics modelling is the knowledge about the nature of gradients and processes, and their effect on plant development.

*Characteristic gradients and processes of riparian landscapes*
Compared to the situation in adjacent uplands areas, the regular input of water through flooding, in combination with favourable temperature, air and soil moisture, as well as the accelerated dynamic of litter, are responsible for the longitudinally as laterally increasing fertility of soil in riparian areas (Malanson, 1993; Naiman *et al.*, 1998). Rapid growth and rapid decomposition explain why the riparian forests have high nutrient recycling capacity, which in turn is why generation changes take less time than in upland adjacent areas. Müller and Scharm (1996) underline the importance to consider, in addition to morpho- and hydrodynamics, also nutrient dynamics. Particularly, in the catchment area of the alpine rivers the alluvium is characterized by a lack of nutrients (Heller, 1969; Müller and Scharm, 1996), whereas in the lowland parts of the river finer sediment is deposited including fine

organic material. Therefore, the nutrient capacity is changing following the longitudinal location of the riparian area in respect of the river system. The lateral gradient concerning the accumulation of organic matter and total nitrogen content is related to a decrease of perturbation by flooding and erosion (Heller, 1963; Amoros and Wade, 1993; Müller and Scharm, 1996).

Apart from nutrient scarcity even drought can limit species development in riparian areas; particularly in the early successional stages of alpine rivers with a higher geomorphological activity (Ellenberg, 1996; Siegrist, 1913). The freshly deposits are mainly of coarse structure with a low amount of fine sediments and organic matter, resulting in a low water retention capacity. If at the same time the groundwater level can not be reached by the roots of young saplings, drought stress will affect strongly plant development (Bayard and Schweingruber, 1991; Patz, 2000). Following Tabacchi *et al.* (2000) several studies confirm the use of groundwater by adult riparian trees, in opposition to other water sources such as precipitation (Snyder and Williams, 2000) they were depending on during the establishment phase (Dawson and Ehleringer, 1991). The lateral gradients due to hydraulic and geomorphologic processes belong to the most important gradients. Flooding can affect development of woody plants physiologically and mechanically. The lack of oxygen during flooding periods affects vital physiological functions and metabolic pathways and is expressed in symptomatic terms by a decline in growth or even the death of woody plants (Glenz *et al.*, 2005a; Chapter 2), whereas short but powerful flooding events may cause uprooting or stem breakage (Broadfoot and Williston, 1973; Malanson, 1993). On the other hand, geomorphological processes (erosion and deposition) can go along with the hydraulic processes by increasing mechanical stress due to a reduction of tree stability or by affecting vital physiological functions due to burial by sediments (Naiman and Décamps, 1997; Bendix and Hupp, 2000). However, geomorphological processes create also suitable nursery sites for many riparian woody species (Gurnell *et al.*, 2001). Riparian tree and shrub species, particularly *Salix* spp., *Populus* spp. are adapted to changing hydrogeomorphological conditions by developing typical species-specific life history strategies such as rapid height and root growth (Johnson, 1994), tolerance to nutrient scarcity and burial, release of large numbers of seeds following peak flows, rapid germination, lack of seed dormancy, and capability of vegetative reproduction particularly after damage (Heller, 1969; Johnson, 1994, 2000; Naiman *et al.*, 1997; Scott *et al.,* 1997). Developments of morphological, anatomical and physiological adaptations to submersion were described in Glenz *et al.* (2005a; Chapter 2). Following Bendix and Hupp (2000) the transversal distributional pattern of riparian woody vegetation may be limited by the tolerance of a species for specific disturbance or stress regimes, as well as by tolerance for other more subtle interactions, including interspecies competition.

The main direct effect of vegetation on hydraulic processes manifests itself through an increase of roughness parameters and a resulting reduction of flow velocity. The roughness of vegetation depends on its height and stiffness coefficients, a composite parameter that includes elasticity and shape of the vegetation (*e.g.* Fathi-Maghadam and Kouwen, 1997). Thorne *et al.* (1997) emphasize the importance of including the shape and biophysical characteristics of plant species, and also seasonal and sucessional plant dynamics in hydraulic studies of overbank flows. Some recent studies have adopted a species-based approach, which takes into account the biological characteristics of particular plants in the computation of hydraulic parameters (Fathi-Maghadam and Kouwen, 1997; Freeman *et al.*, 2000). In summary, the dynamics of natural fluvial landscapes and the complexity of interacting driving-processes responsible for the riparian forest dynamics require a coupled model approach of an ecological, hydraulic and geomorphological model.

*Vegetation dynamics modelling*
Forest succession models are well suited for examining vegetation response to changing environmental conditions. Examples include gap models (Botkin, 1993; Bugmann, 1994) or distribution-based forest succession models (Lischke *et al.*, 1998), which simulate forest succession considering the interrelationships among vegetation elements and including process-based approaches that account for competition as well as for the interaction with the abiotic environment (*e.g.* nutrient availability). In opposition to statistic models which refer to the static equilibrium concept (Bolliger *et al.*, 2000), the expression of plant response to the environment is in such models not limited to reproduce present day conditions (Shugart and Prentice, 1992). However, these dynamic models were mainly applied to upland conditions (*e.g.* ForClim, Bugmann, 1994; ForSum, Kräuchi, 1994, ForEce, Kienast, 1987), except in the studies of Pearlstine *et al.* (1985) and Phipps (1979). Indeed, Pearlstine *et al.* (1985) developed a bottomland hardwood succession model (FORFLO) to study the impact of an altered hydrologic regime on the growth and succession of coastal forested floodplain in South Carolina, US. The model SWAMP (Phipps, 1979) aimed to simulate the forest vegetation dynamics of southern wetlands in Arkansas, US. However, these models are not conceived for river systems found in Central Europe and do not address environmental influences typical for riparian systems, like nutrient scarcity, mechanical disturbance or drought stress explicitly. Furthermore, both models do not cover integrally the main responsible biotic and abiotic factors implicated in species response to flooding nor the influence of vegetation on hydraulics. For instance, colonization by woody species can reduce flow velocity on a site by an increased roughness.

A coupled model approach of dominant driving-processes, although recognized as important (Malanson, 1993), is not yet available at the desired temporal and spatial scales. Moreover, simulations of riparian forest dynamics for Central European conditions using process-based approaches have never been done so far. However, coupled model approaches would be needed for a better theoretical understanding of the riparian systems functioning or, from a management point of view, to predict the ecological consequences of river management measures.

In this paper, we present a new riparian forest dynamics model, referred to as RIFOD, coupling an ecological model to a hydraulic model. The current model version allows simulating short or long-term riparian forest dynamics at an appropriate spatial scale, for riparian areas in which the geomorphological activity of the river is not a dominant driving-process (*e.g.* lowland rivers) or in case of restoration projects, for widened fluvial corridors with morphologically stable stream channels (*e.g.* minor river bed is stabilized by hydraulic engineering structures). Simulation of riparian forest dynamics under different hydraulic conditions can be a helpful tool in the decision-making process of large river restoration projects or the planning of retention basins, for instance by opposing their ecological gain to the land used. Behaviour of RIFOD is illustrated at the 3rd Rhone Correction Project in Valais (Switzerland).

# DEVELOPMENT OF THE RIFOD MODEL

The model RIFOD, standing for 'RIparian FOrest Dynamics', couples an adapted forest succession model (*i.e.* ecological model) with a hydraulic model. The model is spatially-explicit concerning the interactions of the ecological and hydraulic processes and is applied on a 10 times 10 m mesh grid of defined latitudinal and longitudinal extensions; see schematic representation in Figure 1. In what follows, the ecological and hydraulic models are described. For easier reading, all explicit notations of time and spatial dependences in subsequent equations will be avoided.
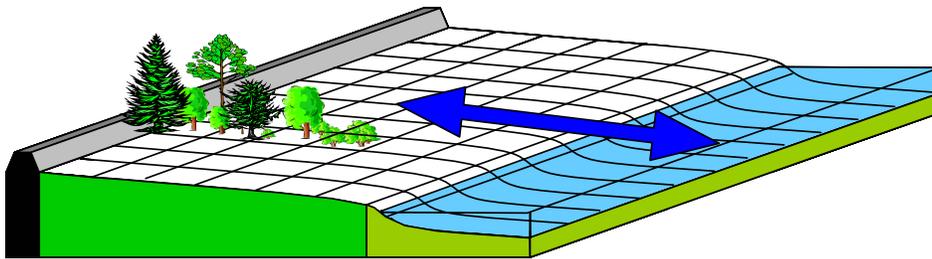


Figure 1: Schematic representation of RIFOD's model domain.

## A. ECOLOGICAL MODEL

The ecological model is based on elements of different forest succession models, which were improved, adapted and complemented at the process level in regard to the ecological gradients and processes in riparian areas. It is organized in a modular manner: RIFOD-P stands for the population dynamics module, RIFOD-W for the soil water balance module, RIFOD-N for the soil nitrogen dynamics module and RIFOD-F for the flooding stress module. The modules are interacting and the coupling of the ecological model with the hydraulic model is assured by model interfaces. Figure 2 illustrates the structure of the ecological model with the modules calculating the environmental stress factors and their influence on the population dynamics module, as well as the parameters exchanged between these modules.
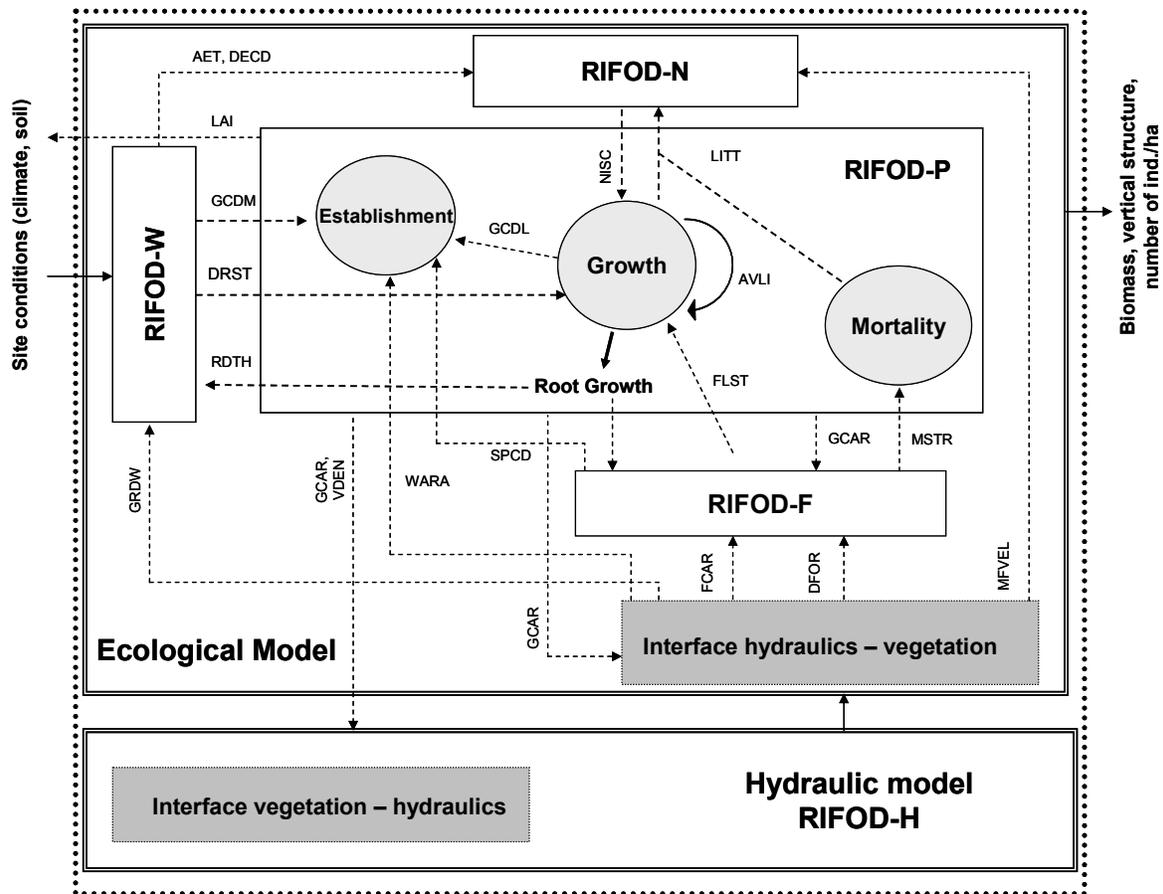
Figure 2: Conceptual representation of the ecological model structure with the modules (RIFOD-W, RIFOD-N, RIFOD-F) calculating the environmental stress and their influence on the population dynamics module RIFOD-P and the variables exchanged between these modules. RDTH; rooting depth, GCDM, moisture germination conditions, GCDL; light germination conditions, DRST; drought stress (*i.e.* soil moisture growth factor; SMGF), NISC; nitrogen scarcity (*i.e.* soil nitrogen growth factor; SNGF), LITT; litter production, GCAR; geometrical plant characteristics (*e.g.* crown height), MSTR; mechanical stress, SPCD; sprouting conditions, FLST; physiological flooding stress (*i.e.* flooding growth factor; FLGF), FCAR; flooding characteristics (*e.g.* flooding duration), DFOR; drag force, GRDW; groundwater level, VDEN; vegetation density, MARA; wetted area. AVLI; light availability, MVEL; maximal flow velocity, LAI; leaf area index, AET; actual evapotranspiration, DECD; conditions of denitrification.

The model integrates 65 Central European tree and shrub species – not all being typical riparian species. This allows the consideration of scenarios by which species composition may change into a more xeric upland composition due to modified site conditions resulting for example of new management decisions (*e.g.* lowering of discharge). Following the ecological model is presented in more detail.

## A. 1 Population dynamics

Population dynamics of RIFOD-P is calculated based on the spatially explicit distribution-based, height-structured forest succession model TreeMig (Lischke *et al.*, 2005). In opposition to individual-based GAP models (*e.g.* JABOWA, Botkin, 1993; ForClim, Bugmann, 1994; ForEce, Kienast, 1987), TreeMig is aggregating the continuous height distribution of individual trees on many patches into a height-structured tree population with theoretical random dispersion over the whole simulated forest area, in order to capture the stochastic variability within a forest. Note that this was already the case with the local model DiscForM (Lischke *et al.*, 1998). Vertically, horizontally and temporally changing distributions of tree tops are simulated by frequency distributions based on a Poisson distribution. These determine the spatial distribution of the light intensity within the stand by influencing inter- and intraspecific competition for light throughout the forest. Light intensity, in turn, affects the process rates of growth, death and establishment. According to Lischke *et al.* (1998) the resulting population dynamics model for species $s$ at height class $i$ for a time interval of one year is given by

$$\Delta N_{s,i} = -D_{s,i} + G_{s,i-1} - G_{s,i} + B_{s,i},$$

where $\Delta N_{s,i}$ is the change of the population density per patch area (Ind./m$^2$yr), $D_{s,i}$ denotes the death (Ind./m$^2$yr) and $B_{s,i}$ the birth (Ind./m$^2$yr). $G_{s,i-1}$ corresponds to the individuals entering height class $i$ from height class $i$-1 (Ind./m$^2$yr) and $G_{s,i}$ to the number of individuals leaving height class $i$ by outgrowing (Ind./m$^2$yr). Birth is restricted to the lowest height class ($i$=0). For details see Lischke *et al.* (1998).

### Plant growth
Based on the relationship of Moore (1989) the yearly diameter increment of tree and shrub species is calculated for each height class, depending on the environmental conditions and the light availability and is given by

$$\frac{dDBH_{s,i}}{dt} = f(L) \cdot \frac{Gr_s \cdot DBH_{s,i} \left( \frac{1 - H_{s,i}}{H_{\max_s}} \right)}{274 + 3b_{2,s} DBH_{s,i} + 4b_{3,s} DBH_{s,i}^2} \cdot f(E),$$

where $f(E) = FLGF_{s,i} \cdot \sqrt[3]{SMGF_{s,i} \cdot SNGF_s}$,

$$b_{2,s} = \frac{2 \cdot (H_{max(s)} - 137)}{DBH_{max(s)}} \quad \text{and} \quad b_{3,s} = -\frac{b_2}{2 \cdot DBH_{max(s)}}.$$

Here, $dDBH_{s,i}$ is the change in diameter at breast height (m) in one year for trees and shrubs of species $s$ in height class $i$, $DBH_{max}$ and $H_{max}$ denote the maximum diameter at breast height (m) and the maximum height (m) of species $s$, $Gr_s$ is a constant growth parameter (m/yr), $b_{2,s}$ and $b_{3,s}$ are parameters expressed as functions of $DBH_{max}$ and $H_{max}$, $f(L)$ denotes the effect of available light on growth (at height class $i$) and $f(E)$ the effect of the environmental constraints ($FLGF_{s,i}$, $SMGF_{s,i}$, $SNGF_s$), which will be described below. Corresponding height increment as well as the number of trees and shrubs of species $s$ entering and outgrowing height class $i$ are calculated based on Lischke *et al.* (2005).

Values of $DBH_{max}$, $H_{max}$ are based on Bugmann (1994), Amann (1954), Prentice and Helmisaari (1991), Geyer (1997), Becker (1982), Godet (1986), Bartels (1993), Bernatzky (1978) and others. Values of shrub species for which no value could be assigned for $DBH_{max}$, were set to 0.2 m. The species parameters are listed in the Appendix.

## Plant mortality

The death rate (yr$^{-1}$) for species $s$ at height class $i$ includes an age related and a stress related mortality. A stress related mortality in case when a tree fails to realize a specified minimum diameter increment for a number of successive years (Lexer and Hönninger, 2001) due to unfavourable environmental conditions (*e.g.* drought, shade), but also mechanical stress due to flooding.

## Plant recruitment (birth)

In TreeMig reproduction of a species depends on the availability of seeds in the seed bank and therefore on the seed producing trees and the dispersal of the yearly produced seeds. In RIFOD-P seed production and seed dispersal are not explicitly modelled but represented by a seed input adapted in relation to the thousand corn weight of a species. The latter is a proxy for the life-history strategy (*e.g.* dispersal strategy, quantity of seeds produced, vulnerability at the establishment phase) and involves the assumption of a more or less constant tree parent population in the neighbourhood. Regeneration is split into the processes of seed inflow (*i.e.* finally

remaining seed input after perturbation by water), seed bank dynamics, germination, asexual reproduction and sapling development.

*Sexual reproduction*

To consider differences of seed input into the patches due to different life-history strategies, a linear regression model has been fitted ($R^2$=0.804) on the log-transformed data of Rohmeder (1972) relating the number of seeds/m$^2$ ($S_s$) to the thousand corn weight ($TCW_s$; g) of several species $s$, resulting in

$$\log\left(S_s\right) = 4.019 - 0.6255 \cdot \log\left(TCW_s\right).$$

Norming seed input of each species $s$ by the highest seed input recorded, a species specific seed input rate is calculated. Success of establishment of riparian species depends on the interaction of water levels and timing of seed dispersal (van Splunder *et al.* 1995; Johnson, 2000). Following Rohmeder (1972) this is considered as the seed falling period. Assuming a constant distribution of the seed input *(SI_s)* over the dispersal period of each species $s$, the final amount of yearly remaining seed inflow is determined distinguishing the case of increasing and decreasing daily water level expressed by the fraction of wetted area $F_d$ of the patch during the dispersal period at day $d$. The seed inflow $I_{s,d}$ of species $s$ at day $d$ is given by

$$I_{s,d} = \begin{cases} \left(I_{s,d-1} + SI_{s,d}\right) \cdot \left(1 - F_d\right), & if \;\; F_d > F_{d-1}, \\ I_{s,d-1} + SI_{s,d} \cdot \left(1 - F_d\right), & else. \end{cases}$$

The seed bank, *i.e.* all seeds which are available for germination in each cell, is increased by seed inflow and reduced by three processes: germination, loss of germinability and loss of seeds.

In riparian areas, success of germination depends particularly on light and moisture conditions. Seeds of *Salix* spp. and *Populus* spp. are only shortly viable and need sufficient moist conditions to germinate. Therefore, a moisture germination rate is calculated considering that species with a very low TCW$_s$ (< 1 g) are more drought sensitive than species with a higher TCW$_s$ (> 1 g), due to a lack of water and nutrient reserves in the seeds. Following Rohmeder (1972), TWCs expresses vulnerability to environmental stress factors at the first year of development. Limits of favorable moist conditions calculated at a daily basis are set at a pressure head of 80 cm of the

top soil horizon used in RIFOD-W. Following Kozlowski (2002), germination capacity decreases rapidly as the soil dries below field capacity. Species with $TCW_s$ < 1 g require consecutive moist conditions (Moss, 1938), whereas others are assumed to be more tolerant to fluctuating moisture conditions. On the other hand, moisture germination rate of $TCW_s$ < 1 g increases more rapidly in case of favorable conditions. Therefore the following relationship is used to determine the moisture germination rate $m\beta_s$ (yr$^{-1}$) of the two TCW classes:

$$m\beta_s = 1 - \left( \frac{Vp - G_{max}}{Vp} \right)^{\alpha_w}$$

where $Vp$ is the length of growing season (d), $G_{max}$ the maximal length of favourable moisture germination condition (d) and $\alpha_w$ the corresponding coefficients for the TWC classes. Successful germination of a species $s$ occurs in case of $r_1 < gp_s$, where $r_1$ is a random variable between [0,1], $lt\beta_s$ denotes the light germination rate (yr$^{-1}$) and $gp_s$ the successful germination rate (yr$^{-1}$), *i.e.*

$$gp_s = \min \left( m\beta_s, lt\beta_s \right)$$

Finally, the number of individuals per germinating species depends on an establishment rate, which is influenced by browsing, moisture conditions and light, the latter averaged over all light conditions in the stand; see Lischke and Löffler (2005) for details. The values of the beginning and ending of the dispersal period were set based on data of Rohmeder (1972) and Amann (1954). For the remaining species the maturity period has been considered by adding three months for species with larger fruits. For these species we consider that the dispersal/falling period follows directly the period where the seeds are mature (Rohmeder, 1972). Maximum seed age is a parameter taken on the model TreeMig; see Lischke and Löffler (2005). For the added species in RIFOD, data about maximum seed age is estimated based on quantitative and qualitative data. For the *Salix* spp. and *Populus* spp. maximum seed age has been set to 0.5 year; as several authors (*e.g.* Splunder *et al.*, 1995; Ellenberg, 1996) pointed out their short seed viability. For the species for which no data could be obtained, mostly shrub species as *Viburnum* spp. or *Crataegus* spp., a default value of 2 years was considered. The seed germination rate was again based on TreeMig. For the species with no data a default value of 0.5 was assigned. The same holds for the amount of seed loss which was set to 0.8.

*Asexual reproduction*

Asexual reproduction or vegetative reproduction, such as root and trunk suckering, as well as the ability to sprout from transported plant fragments (*e.g.* rhizomes, branches) reported particularly for *Salix* spp. and *Populus* spp. (Gurnell *et al.*, 2001), is modelled as a stochastic process. Root suckering occurs from increased stress due to submersion, trunk sprouting after death of an individual tree or shrub due to mechanical disturbance. Reproduction by root and trunk suckers is also possible in limiting light and water availability conditions (Koop, 1987). This presents an advantage to the sexual reproduction strategy. However, the number of sprouts from plants fragments transported by the river depends on the fraction of the maximal wetted surface and on the light conditions of a patch, as this way of reproduction has been observed mainly on bare ground. Data whether the tree or shrub species have the ability to respond by sprouting by an above-cited type were based on Schiechtl (1992), Ehlers (1960), Lange and Lecher (1993), Koop (1987), Karrenberg *et al.* (2002) and Kräuchi (1994).

*Sapling development*

The number of trees which can maximally establish and become saplings with a height of 130 cm in the first height class is limited to 3200 stems/ha. This corresponds to an average value of the amount recorded by the Swiss national forest inventory 1993-95 for trees from 70-129 cm height (Brassel and Brändli, 1999). This limitation can be understood as the inter-specific competition for space of the young saplings. The available space (stockable area per patch) is calculated by multiplying patchsize by a factor that describes the fraction of the patch permanently wetted during the growing season and the fraction of boulders present. Note, that no inter-specific density regulation as in TreeMig was required, because seed input was independent of parent individuals and thus no positive feedback between parent individuals and saplings existed.

## A. 2 Environmental stress factors

The process functions of RIFOD-P depend on several environmental stress factors, namely drought stress, nitrogen scarcity and flooding.

### A. 2. 1. Drought stress
The submodul RIFOD-W is based on the soil water balance model of Kräuchi (1994) used in his model FORSUM. Soil water content is calculated for each day and

considers inputs as canopy throughfall, groundwater and outputs, as root water extraction and drainage. To do so, the hydraulic properties *(e.g.* unsaturated water conductivity, pressure head, water stockage) are calculated for each soil horizon based on the equations of van Genuchten (1986). The pressure head $h$ in function of the soil water content $\theta$ in each horizon $hz$ is determined using the water release curve defined by

$$h\left(\Theta_{hz}\right) = \frac{1}{\alpha_{hz}} \cdot \left[1 - \left(\frac{\Theta_{s,hz} - \Theta_{r,hz}}{\Theta_{hz} - \Theta_{r,hz}}\right)^{\frac{1}{m_{hz}}}\right]^{\frac{1}{n_{hz}}} \quad \text{for } \theta > \theta_r \text{ else } h(\theta_{hz}) = -\ 16000\ cm$$

where $\theta_{r,hz}$ is the residual water content (cm³/cm³), $\theta_{s,hz}$ the saturated water content (cm³/cm³), $\theta_{hz}$ denotes the actual water content (cm³/cm³) and $\alpha_{hz}$, $n_{hz}$ and $m_{hz}$ are empirical parameters for horizon $hz$. The empirical parameters as well as the soil hydraulic data ($\theta_r$, $\theta_s$, $k_s$) were calculated using the pedotransferfunctions of Rawls and Brakensiek (1985), which translate existing surrogate data (*e.g.* particle-size distributions, porosity) into soil hydraulic data. Then, for each horizon $hz$ a root extraction term $S_{hz}$ is calculated, depending only on the soil water pressure head $h$ and a maximal extraction rate $S_m$ (van Genuchten, 1986).

$$S_{hz} = \alpha\left(h_{hz}\right) \cdot S_{m,hz}$$

with the maximal extraction term $S_{m,hz}$ being, $S_{m,hz}(z) = PET \cdot \lambda(z)$, where $\lambda(z)$ is a depth-dependent root distribution function limited at the average rooting depth of the patch. To determine the average rooting depth of a patch, the root growth equation of Glenz *et al.* (2005d; Chapter 5) is used, calculating rooting depth of species $s$ in height class $i$, as a function of drought stress and shading. The vertical root depth increment (cm) in dependence of stem diameter increment at breast height (cm) is

$$\frac{dRD_{s,i}}{dDBH_{s,i}} = -RD_{\max,RT} \cdot E_{F,s,i} \cdot c_s \cdot \exp\left(c_s \cdot DBH_{s,i}\right)$$

where

$$E_{F,s,i} = \left\{ Max_R - \left( Max_R - 1 \right) \cdot SMGF_{s,i} \right\} \cdot \sqrt[3]{LGF_{s,i}} \; ,$$

and $RD_{max,RT}$ is the maximal vertical rooting depth of a species $s$ of rooting type $RT$ (cm), $c_s$ a negative species-specific regression coefficient, $E_{F,s,i,}$ represents the environmental conditions affecting root growth, $DBH_s$ the actual diameter at breast height (cm), $Max_R$ a maximal increment rate and $SMGF_{s,i}$ and $LGF_{s,i}$, denote the soil moisture and light growth factors for species $s$ at height class $i$. The relation for $E_{F,s,i}$ considers the presence of a hydrotropic stimulus. Hence, drought is enhancing vertical root growth development. In absence of this stimulus drought would reduce vertical growth (Glenz *et al.,* 2005d; Chapter 5). Rooting depth is limited by the mean groundwater level at the growing season and the soil depth. Groundwater level is supposed to correspond to the river water level (Soutter, 1996; Piégay *et al.*, 2003). Potential evapotranspiration (PET) (cm) can be calculated following the Penman-Monteith equation (Monteith, 1975) or is read from a climatic input data file. The Penman-Monteith equation allows considering the plant-soil water-relationship feedback through the exchange of the leaf area index calculated in RIFOD-P. Daily root extraction is supposed to correspond to the daily actual evapotranspiration (AET). When soil moisture is limiting, root water extraction is reduced by a factor $\alpha$, which is a function of the pressure head $h$ (Mathur and Rao, 1999; Feddes *et al.*, 1978). The reduction function, obtained by imposing the three conditions listed below, is shown in Figure 3.



$$a(h) = \frac{h - h4}{h3 - h4}, \quad \text{for } h4 \leq h < h3,$$

$$a(h) = 1, \quad \text{for } h3 \leq h < h2,$$

$$a(h) = \frac{h - h1}{h2 - h1}, \quad \text{for } h2 \leq h < h1.$$
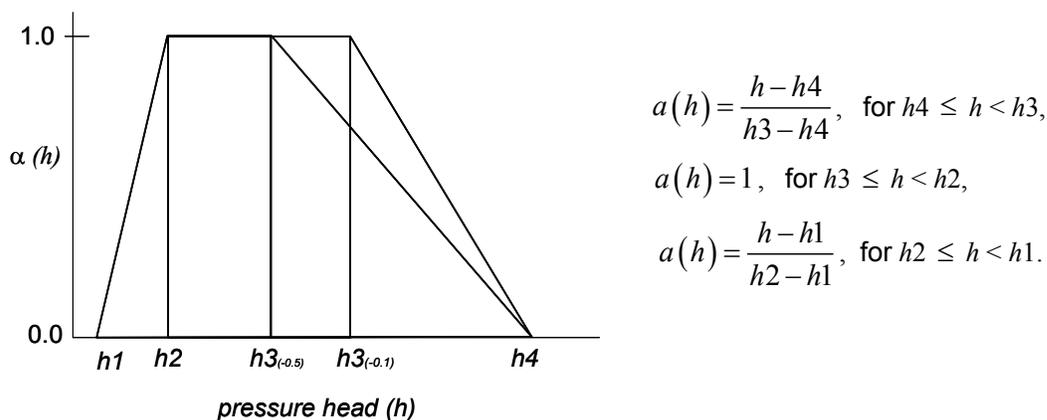
Figure 3: Reduction function $\alpha(h)$ versus pressure head ($h$).

The water extraction is assumed to be zero when the soil is wetter than a certain anaerobiosis point (*h1*=-10 cm) and when the soil is drier than the wilting point (*h4*=-

16000 cm). The water uptake is constant and maximal when the water potential ranges between $h2$ (=-25 cm) and $h3_{-0.5}$ (= -320 cm), respectively $h3_{-0.1}$ (=-600 cm) (Feddes, 1978). At conditions of higher evaporative demand (PET > 0.5 cm) a drop in water uptake generally occurs at higher pressure head values than under conditions of low demand. Next, the unsaturated water conductivity $k$ required to determine drainage from one horizon to another is calculated again according to van Genuchten (1986) by

$$k(s_{e,hz}) = k_{s,hz} \sqrt{s_{e,hz}} \left[ 1 - \left\{ 1 - \left( s_{e,hz} \right)^{1/m_{hz}} \right\}^{m_{hz}} \right]^2$$

$$\text{with } s_{e,hz} = \frac{\Theta_{hz} - \Theta_{r,hz}}{\Theta_{s,hz} - \Theta_{r,hz}},$$

where $s_{e,hz}$ corresponds to the reduced water content (cm$^3$/cm$^3$), $k_{s,hz}$ to the saturated hydraulic conductivity and $m_{hz}$ to an empirical parameter. When the mean pressure head $h$ in the main rooting zone containing most of the fine roots (= 20 % of the average rooting depth) drops below -2000 cm (Kräuchi, 1994), and when the tree and shrub species $s$ in the different height classes $i$ do not reach the groundwater by their roots, a restricted growth unit (RGU) (d) is attributed for that day. The total number of dry days during the growing season is calculated as the overall sum of restricted growth units divided by 3, assuming that three restricted growth units equal one dry day. The soil moisture growth multiplier for species $s$ and height class $i$ is then calculated by

$$SMGF_{s,i} = \frac{\sqrt{D_{3,s} T_{GS} - \left( \dfrac{RGU_{s,i}}{3} \right)}}{D_{3,s} T_{GS}} \quad \text{, where } D_{3,s} = T_{GS} \cdot DrTol_s \text{ with}$$

$T_{GS}$ denoting the length of growing season (d) and $DrTol_s$ a species-dependent drought resistance parameter.

### A. 2. 2. Nitrogen scarcity

Nitrogen availability calculated in RIFOD-N is based on FORCLIM-S (Bugmann, 1994), which is based on Pastor and Post (1985). The model differentiates between

a litter compartment and a humus compartment. Based on the output of the RIFOD-P module, yearly litter production is calculated using empirical allometric relationships, differentiating between three foliage litter types (slow, medium and fast decaying), twig, root and stem litter. Woody stem litter produced by the dead trees in each height class is calculated by the allometric relationships of Perruchoud (1996). In the litter compartment decomposition of the yearly created litter cohorts is calculated. For foliage and root litter the decomposition of the organic matter is predicted from the lignin to nitrogen ratio of the tissue and AET calculated in RIFOD-W. According to Bugmann (1994), AET can be used to characterize the humidity as well as the temperature of the organic soil layer. Moreover, stem and twig litter decay at constant rates. In riparian areas drying and rewetting cycles enhance decomposition of foliage by mainly physical fragmentation. Thus, an enhanced decomposition of foliage litter in flooded patches by 20 % is supposed (Lockaby *et al.*, 1996). The amount of nitrogen immobilized per unit organic matter respired is calculated for each litter type, as well as gross nitrogen immobilization, the amount of nitrogen leaching from the litter and the net immobilization rate of nitrogen. A litter cohort is transferred to the humus compartment when its current nitrogen concentration exceeds the critical nitrogen concentration of the corresponding litter type. Loss of litter due to flooding was considered by relating maximal water flow velocity to the fraction lost of each litter cohort $c$ as follows:

$$LOM_c = \left(1 - \delta_{lt} \cdot v_{max}^{\ 2}\right) \cdot LOM_c ,$$

where $LOM_c$ is the litter organic matter (t/ha) for litter cohort $c$, $v_{max}$ is the yearly maximal water velocity (m/s) and $\delta_{lt}$ denotes the coefficient for each litter type $lt$. In case of litter presence in the soil, nitrogen mineralization is calculated based on the nitrogen/carbon ratio of the litter and the amount of humus organic matter; a constant nitrogen mineralization rate is assumed otherwise. The turnover of humus organic matter is assumed to be proportional to the turnover of humus nitrogen. Next, the amount of nitrogen available for plant growth $AvN$ (kg/ha), is calculated by

$$AvN = \max\left(\triangle HN - Nimb, 0\right) + ExtN$$

where $\triangle HN$ is the net mineralization (t·ha·yr$^{-1}$) for a time interval of one year, $Nimb$ denotes the net nitrogen immobilization (t·ha·yr$^{-1}$), $ExtN$ is an external nitrogen input rate composed by atmospheric nitrogen and river/groundwater nitrogen (t·ha·yr$^{-1}$). Following the river type a constant input of nitrogen during flooding or rising of

groundwater can be added. For example, in case of alpine rivers, deposits present generally no valuable nitrogen input or no enrichment of the nitrogen household (Heller, 1969). Due to the presence of high groundwater levels that may produce the anoxic conditions riparian areas contain typically potential hotspots of denitrification. The loss of daily available nitrogen via denitrification is calculated based on Grundmann and Rolston (1987) and Parsons *et al.* (1991) using

$$F = k_1 \theta f_w f_T C_w AvN \,,$$

$$C_w = 24.5 + 0.0031 \cdot C_s \,,$$

$$f_w = \begin{cases} \left( \dfrac{\left( \dfrac{\theta}{\theta_s} \right) - 0.62}{0.38} \right)^{1.74} & , \text{if } \left( \dfrac{\theta}{\theta_S} \right) > 0.62, \\ 0 & , \text{ otherwise,} \end{cases}$$

where $F$ is the denitrification rate (mg/m$^3$ of soil per day), $k_1$ the denitrification rate coefficient (kg soil/mg C per day), $\theta$ denotes the volumetric water content (m$^3$ H$_2$O/m$^3$ soil), $f_w$ the empirical water function accounting for the degree of anaerobic development, $f_T$ the empirical soil temperature function, $C_w$ is the water soluble organic carbon concentration (mg C/kg soil), $C_s$ the total soil organic carbon concentration (mg C/kg soil) and $AvN$ denotes the available nitrogen (mg/m$^3$). The volumetric water content $\theta$ of the two top horizons, as well as the number of days the anoxic conditions for denitrification are fulfilled, is calculated directly within RIFOD-W. The final amount of available nitrogen is calculated by subtracting the amount of nitrogen lost by denitrification.

The soil nitrogen growth factor representing the influence of nitrogen availability $AvN$ on tree growth rate is calculated using

$$SNGF_s = \max \left[ 1 - \exp \left\{ N_{1,Ntol_s} \cdot \left( AvN - N_{2,NTol_s} \right) \right\}, 0 \right]$$

where $N_{1,kNTols}$ (<0) and $N_{2,NTols}$ are parameters depending on the nitrogen tolerance class of the tree or shrub species NTol$_s$ (Bugmann, 1994, Table 3.13).

## A. 2. 3. Flooding

Flooding affects the plants in two different ways: (a) by creating abiotic conditions for the physiological stress and (b) by exerting mechanical stress – both calculated within RIFOD-F.

*a. Physiological flooding stress*

Flooding stress response is modelled in RIFOD-F based on Glenz *et al.* (2005c; Chapter 4) by applying the fuzzy set theory to flooding stress modelling of Central European tree and shrub species, as well as their classification into flooding tolerance classes done by Glenz *et al.* (2005b; Chapter 3). Fuzzy rules, developed for five flooding tolerance classes, relate the input variables 'flooding duration', 'flooding depth' and 'time since last flooding' to the control variable 'flooding stress response', resulting in the defuzzified output value 'flooding growth factor' (FLGF). Figure 4 represents the membership functions defined for the input and control variables. Duration of flooding is considered as the ratio between the number of days within the growing season where soil is submerged (wetted area > 20 % of patch surface) by water and the duration of the growing season. For 'flooding depth' a distinction is made between 'shallow' (*i.e.* soil submersion), 'medium' (*i.e.* partial submersion) and 'high' (*i.e.* complete submersion). The absolute flooding depth corresponds in this case to the maximal flooding depth (m) of a specific flooding event. This flooding depth needs to be transformed into a relative flooding depth according to the height (and crown length) of a corresponding tree or shrub. Flooding duration, maximal flooding depth and time since last flooding are calculated only within the growing season as flooding within the dormant season is less harmful due to the minimal demand for oxygen by roots and micro-organisms. The influence of the aforementioned abiotic factors on flooding tolerance has been extensively discussed in Glenz *et al.* (2005a; Chapter 2).
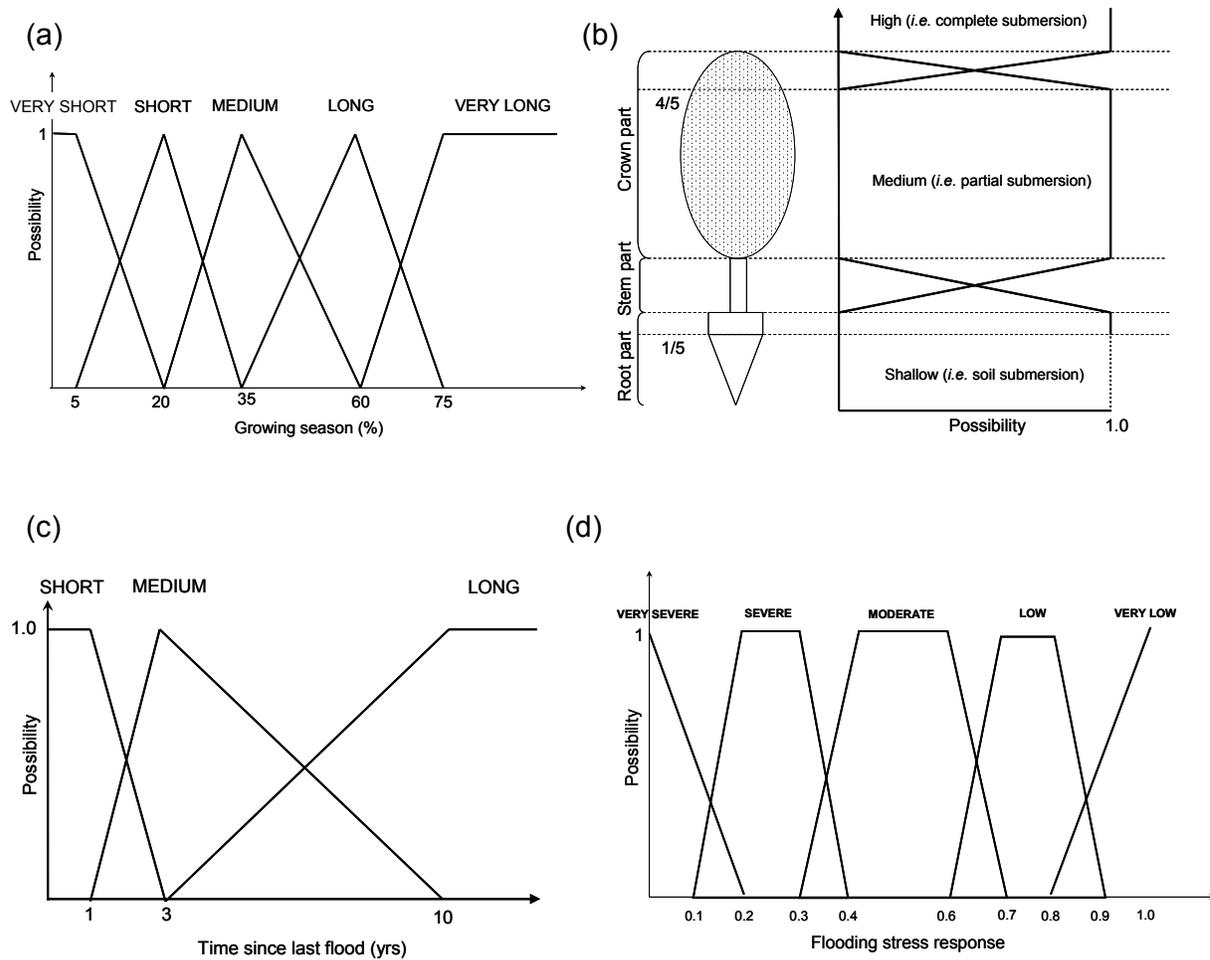
Figure 4: Membership functions for (a) 'flooding duration' (very short, short, medium, long, very long duration), (b) 'flooding depth' (high, medium, shallow inundation), (c) 'time since last flood' (short, medium, long time since last flood) and (d) 'flooding stress response' (control variable) (very severe, severe, moderate, low, very low flooding stress).

## b. Mechanical flooding stress

Mechanical resistance to failure characteristics (*e.g.* stem breakage, uprooting) of trees due to fluid flow have been studied especially in relation to wind. Nevertheless, as the basic equations are identical many findings can be used in the case of the flow of water. Water flow may cause failure of tree and shrub species either by uprooting or breaking. The resistance to failure caused to uprooting or bending has been studied both experimentally and theoretically and mechanistic models are available; see for example Peltola *et al.* (1999) and Gardiner *et al.* (2000). In fact, the maximum bending moment ($BM$) is the result of a drag force acting on the tree and a

gravitational force due to its mass. In RIFOD-F the maximum bending moment is calculated to determine whether water flow can entrain uprooting or stem breakage of tree and shrub species *s* of height class *i*. It is given by

$$BM_{s,i} = G \cdot \left( H_{F,s,i} \cdot y + G_{F,s,i} \cdot w_{s,i} \right),$$

where $BM_{s,i}$, is the maximum bending moment for species *s* at height class *i* (Nm), $G$ denotes a gust factor, $H_{F,s,i}$ the drag force (N), $G_{F,s,i}$ the gravitational force (N), $w_{s,i}$ the horizontal displacement of the tree (m) and $y$ is the height of water level (m). $G$ is set to 1 as turbulence is not considered. The drag force is calculated in the hydraulic-vegetation interface; see page 108. To approximate the projected area $A_{s,i}$ required in the drag force calculation, the geometrical characteristics of a tree or shrub of species *s* at height class *i* are determined, based on crown heights, crown and stem areas and the assumptions about the general shape. To do so, crown heights were determined by classification tree analysis on data of the National Forest Inventory of Switzerland (1993-1995; WSL, 2003). In all 72'146 trees of 42 tree and shrub species are recorded with different size and categorical crown, as well as stand (*e.g.* basal area) and site characteristics (*e.g.* altitude, slope). Crown heights were classified in three classes; 'large-crown' trees (=C1), for trees with a crown heights larger then the half tree height, 'medium-crown' trees (=C2), for trees with a crown heights between half to a quarter tree height and finally 'short-crown' trees (=C3), for trees with crown heights shorter then a quarter tree height. Input variables were tree diameter at breast height (cm) (*i.e.* DBH), tree height (m) (*i.e.* H), basal area (m$^2$/ha) (of individuals larger then the observed) (*i.e.* BAL), SDI ('stand density index'), altitude (m.a.s.l.) and slope (%) of the site considered. SDI is a measure of stand density and is based on number of individuals/ha and the mean diameter at breast height (mean of all DBH of a stand). BAL and SDI can be seen as an expression of the competition situation within a specific stand. DBH, H, BAL and SDI are calculated within RIFOD-P. Binary rules of the variables were determined using the S-Plus library rpart, known as 'Recursive Partitioning' (Therneau and Atkinson, 1997). In opposition to the deciduous species, all coniferous species have been grouped. The classification tree analysis did not reveal species type as important for classification into crown heights categories. Deciduous species with only few data have been grouped into 'other broadleaf species', whereas the others into genus type. Figure 5 illustrates an example of a classification tree based model for the *Salix* spp. with a misclassification error of 24.6 %.

A tree-based model for Salix spp.
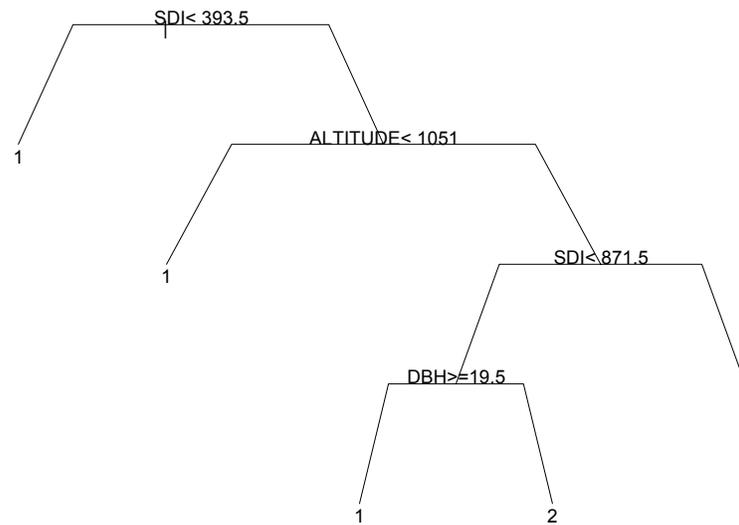


Figure 5: Tree-based model to determine crown length of *Salix* spp.
based on stand and site characteristics.

In order to have a continuous response, final crown lengths were determined by randomly selecting a crown ratio based on the cumulated probability distribution function of the calculated crown heights at the corresponding terminal node. For species with a shrub habit, crown height is equal to plant height. Indeed, as these species have, in opposition to tree species, no shaft and develop branches directly at the lowest stem parts. Crown heights were then also used in RIFOD-F to determine the flooding depth (*e.g.* partial submersion) of a tree or shrub species.

To obtain empirical relationships between the output of forest succession models and the crown diameter, single-tree data from the Swiss national forest health inventory (Sanasilva 1997; Brang, 1998) were evaluated. However, not for every species sufficient data were available. Hence, a distinction has been made between coniferous and deciduous tree species, and within the deciduous species, between species with typically large and smaller crowns. On the aggregated data a non-linear regression model was fitted, with the crown width (m) as response and the diameter at breast height (cm) as input variable. Remaining species were assigned to one of the three types following the indications of Clouston (1990). As data of Sanasilva 1997 cover only trees over a diameter greater then 12 cm, a linear interpolation was made for diameters between 0 and 12 cm. For the shrub species the crown expansion is estimated by a crown dimension factor, relating height of a species to its

crown diameter based on the data of Geyer (1997). For deciduous species a rectangle crown shape and for coniferous species a cone is considered.

Once bending of the tree begins, an additional force – a gravitational force – is exerted by the weight of the tree.

This force is calculated by

$$G_{F,s,i} = M_{s,i} \cdot g$$

where $G_{F,s,i}$ is the gravitational force (N), $M_{s,i}$ the above-ground biomass of a tree or shrub species $s$ at height class $i$ (kg) and $g$ denotes the gravitational constant (=9.81 m/s$^2$). Next, horizontal displacement $w_{s,i}$ corresponds to

$$w_{s,i} = \frac{q \cdot y^4}{MOE_{s,i} \cdot I},$$

where $MOE_{s,i}$ is the modulus of elasticity of a tree or shrub of species $s$ at height class $i$ (N/m$^2$), $q$ denotes the distribution of drag force (N/m), $I$ the momentum of inertia (m$^4$) and $y$ the water level height (m). As the distribution of hydraulic force is considered as uniform $q$ equals $H_F$. The modulus of elasticity is calculated based on the non-linear relationship of Freeman *et al.* (2000), given as

$$MOE_{s,i} = 7.648 \cdot 10^6 \cdot \left( \frac{H_{s,i}}{DBH_{s,i}} \right) + 2.174 \cdot 10^4 \cdot \left( \frac{H_{s,i}}{DBH_{s,i}} \right)^2 + 1.809 \cdot 10^3 \left( \frac{H_{s,i}}{DBH_{s,i}} \right)^3$$

and $H_{s,i}$ is the mean height (m) of a shrub or tree of species $s$ in height class $i$, and $DBH_{s,i}$ denotes the corresponding diameter at breast height (m).

*Uprooting resistance*
The resistance to uprooting is calculated in RIFOD-F based on the study of Peltola *et al.* (1999), where resistance to uprooting was predicted from the estimate of the root-soil plate weight to derive a resistive moment. A tree will be uprooted when the total maximum bending moment exceeds the support provided by the root-soil plate anchorage. This in turn depends on the root-soil plate weight, the depth and the diameter of the root-soil plate, as well as the soil properties. The support provided by

the roots is modelled by the weight of the soil-root plate as a proportion of total anchorage. The latter includes the weight, the strength of the root hinge and the soil strength at the base of the root-soil plate. The maximum resistive bending moment for uprooting $M_{crit,uprooting,s,i}$ (N/m), that a tree or shrub species $s$ of height class $i$ can withstand without being uprooted is defined as

$$M_{crit.uprooting,s,i} = \frac{g \cdot m \cdot RS_{mean,s,i}}{A_{rsw}},$$

where $m$ denotes the fresh mass of the soil-root plate (kg), $RS_{mean,s,i,}$ the mean depth of the root-soil plate of a species $s$ at height $i$ (% of maximum depth of the root system) and $A_{rsw}$ is the dimensionless factor representing the proportion that the root-soil plate weight provides to the total root anchorage. According to Peltola *et al.* (1999) the supporting moment caused by the weight of the root-soil plate ($A_{rsw}$) was assumed to be 30 % of the total below surface support in the case of deep rooting species (*e.g. Pinus sylvestris)* and 20 % for shallow rooting species (*e.g. Picea abies)*. Furthermore, the authors set the mean depth of the root-soil plate volume ($RS_{mean}$) to 21 % of the maximum depth of the root system. The classification into rooting types as well as the calculation of the maximal rooting depth is based on Glenz *et al.* (2005d; Chapter 5). The form of the root system is considered to be a cone as is it often observed on alluvial soils (Kutschera and Lichtenegger, 2002). To calculate the volume of the root-soil plate, horizontal rooting extension is assumed to correspond to crown width (Assmann, 1961; Gardiner *et al.*, 2000).

*Stem breakage resistance*
The resistance to breakage is based on the assumption that the water-induced stress in the outer fibres of the stem is constant at all points between the base of the canopy and the butt swell at the stem base. A tree stem is assumed to break if the maximum bending moment exceeds the stem resistance calculated as a function of diameter at breast height and the modulus of rupture (MOR) (Peltola *et al.*, 1999). Hence, the maximum bending moment $M_{crit,breakage}$ (N/m) that a tree or shrub species $s$ of height class $i$ can withstand without breakage is

$$M_{crit,breakage,s,i} = \frac{\pi}{32} \cdot DBH_{s,i}^{3} \cdot MOR_{s},$$

where $DBH_{s,i}$ is the diameter at breast height (m) of a tree or shrub of species $s$ at height $i$ and $MOR_s$ denotes the modulus of rupture (N/m$^2$) of species $s$.

The modulus of rupture was derived based on Lohmann (1991), Sell (1989), Kollman (1951), Wagenführ and Scheiber (1989), Vorreiter (1949) and Dahms (1996). As no data could be collected for *Salix* species other then *Salix alba*, the value of *Salix alba* was considered to be representative for all *Salix* species. The same is valid for the *Acer* spp. in case of *Acer platanoides*, and for *Prunus padus* and *Prunus domestica* in case of *Prunus avium*. For the remaining species, like *Juniperus communis, Alnus incana* and *Alnus viridis,* a mean value has been calculated (= 91 N/mm$^2$) based on the species for which data were available.

# B. HYDRAULIC MODEL

Lateral variation in hydraulic parameters such as flow depth, flow velocity and shear stress, related to elevation and distance from the river bed is important for the dynamics of vegetation. River hydraulics affects vegetation mechanically through drag force causing uprooting or stem breakage or physiologically by the creation of anaerobic conditions as a consequence of soil or canopy submersion. On the other hand, the main effect of vegetation on hydraulic processes manifests itself through an increase of roughness parameters and a resulting reduction of flow velocity (and increase of flow depth). Vegetation roughness depends on the area of the submerged plant parts and the stiffness coefficient, a composite parameter that includes elasticity and shape of the vegetation. A dynamic and spatially explicit modelling of the vegetation-hydraulics interaction requires the coupling of the forest succession model (*i.e.* ecological model) to a hydraulic model, assured by a vegetation-hydraulics and a hydraulics-vegetation interface module, see Figure 6.
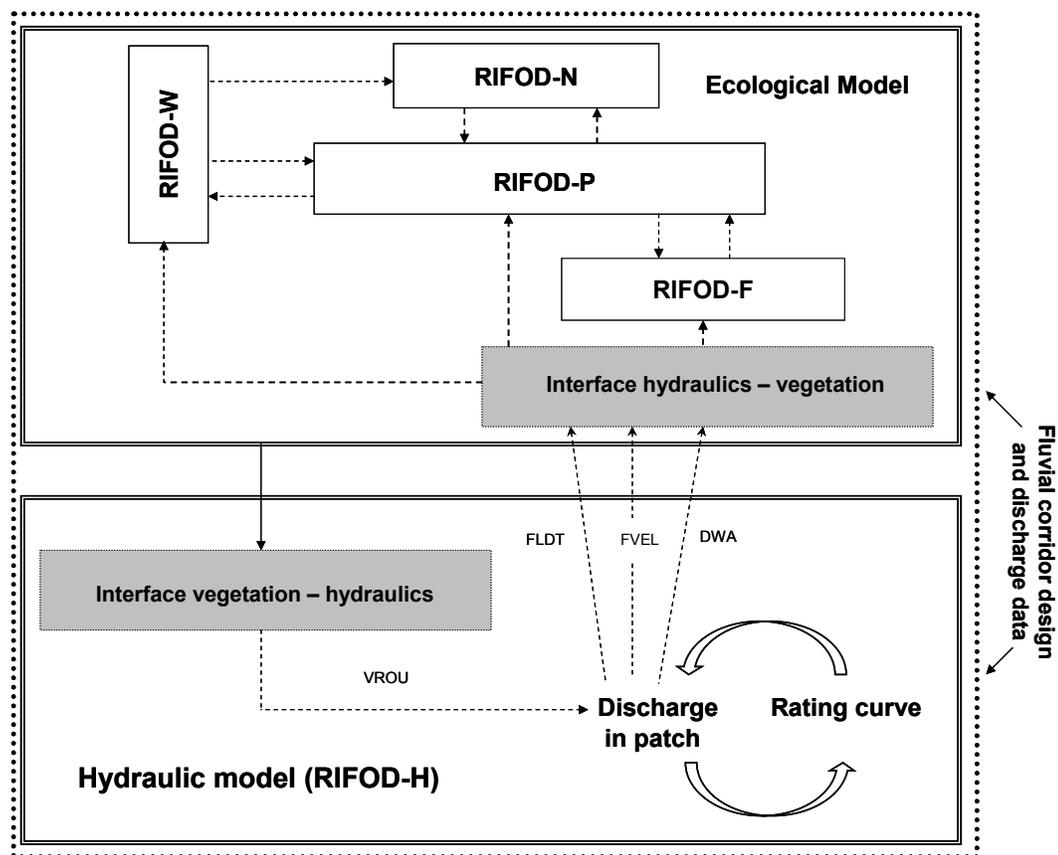


Figure 6: Conceptual representation of the hydraulic model and the coupling to the ecological model. FLDT; flow depth (m), FVEL; flow velocity (m/s), DWA; daily wetted area, VROU; vegetation roughness.

The modular approach of RIFOD allows theoretically coupling a simple or a more complex hydraulic model (3-D) to the ecological model. However, in regard of the model's intended use and the computational time efficiency we use a quasi 2-D approach to calculate flow depth (m) and flow velocity (m/s). Several researchers developed 'Lateral Distribution Models' based on a quasi-2D approach by integrating or averaging the flow on the vertical direction (*e.g.* Ervin *et al*., 2000). These methods assume a uniform steady flow in a prismatic section, accounting for eddy viscosity and secondary flows. The flow domain is divided in sub-domains each having its own geometric and hydraulic characteristics. For each sub-domain an analytical solution for the quasi-1D steady state equation accounting for the eddy viscosity forces and for momentum transfer can be obtained. Herein, we use the implementation of Ervine *et al.* (2000) quasi two-dimensional method by using a quasi steady-state model approach to model hydraulic conditions – emphasizing on the ecological relevant, lateral dimension. A rating curve allows, based on the actual topographic situation and roughness conditions (bed, vegetation), to calculate the water height-water flow relationship. Knowing the daily discharge, the corresponding flow depth in each patch can be determined by interpolation. For a given flow depth the laterally distributed flow velocity integrated over depth, and implicitly discharge in each patch is determined by the hydraulic model. The fluvial corridor geometry as well bed and vegetation roughness are the required inputs of the hydraulic model. The main abiotic factors determining physiological flooding stress such as flooding duration, flooding depth and time since last flooding are calculated, within the hydraulics-vegetation interface, based on the flow depth in each patch.

The direct effect of vegetation manifests itself through the increase of roughness parameter used in the hydraulic model, influencing flow velocity and consequently flow depth. Flow resistance problems are usually classified into rigid and flexible vegetation flow resistance, and within these groups between flow over submerged, short vegetation and flow through non-submerged, tall vegetation. Only recently the vegetation-hydraulics interaction, considering natural flexible vegetation, is becoming a field of active research (Oplatka, 1998; Kouwen and Fathi-Moghadam, 2000). Hence, less is known about the effects of flexible roughness and alterations in flow depth. Moreover, there is only little available field data other than overall roughness coefficients representing limited flow conditions (Järvelä, 2002). Herein we use semi-empirical relationships of Freeman *et al.* (2000), which for a given water level divided vegetation roughness into roughness of flexible elements (crown area) and rigid elements (stem area) in a patch, integrating vegetation characteristics (density, frontal area of plants) provided by the ecological model on a longitudinal range. The

resistance coefficient $V*/V$ required to obtain the friction factor $f$ is calculated for example for partially submerged vegetation by

$$\frac{V_*}{V} = \sum_{i=1}^{s} 3.478E-05 \cdot \left( \frac{E_{s,s} A_{s,s}}{\rho A^*_{i,s} V_*^2} \right)^{0.150} \cdot \left( MA_{i,s}^* \right)^{0.166} \cdot \left( \frac{V_* R_h}{\upsilon} \right)^{0.622}$$

where $A_{s,s}$ is the cross-sectional area (m²) of the stem (or stems) of a tree or shrub of species $s$, $E_{s,s}$ is the modulus of plant stiffness (N/m²) of a tree or shrub of species $s$, $A_{i,s}$ denotes the frontal area (m²) of a tree or shrub of species $s$ blocking flow, $R_h$ is the hydraulic radius, $R_h$ = flow area / wetted perimeter (m), $V$ is the mean channel velocity (m/s), $V*$ denotes the shear velocity (m/s), $M$ is the relative plant density (Ind./m²), $\upsilon$ denotes the fluid dynamic viscosity (m²/s) and $\rho$ the fluid density (kg/m³). The Darcy-Weisbach friction factor $f$ calculated by

$$f = 8 \cdot \left( \frac{V_*}{V} \right)^2 ,$$

affects flow velocity $V$ by $V = \sqrt{\dfrac{8 \cdot S \cdot g \cdot R_h}{f}}$, where $S$ is the longitudinal slope, $g$ denotes the gravitational constant (m/s). A modification of flow velocity influences discharge and consequently flooding depth and duration. As the effect of short-living herbs on roughness is low (Brooks *et al.*, 2000), no supplementary roughness is added to the calculated roughness of shrub and trees.

The drag force $H_{F,s,i}$ (N/m) – force acting on plants in opposition to vegetation resistance – required to simulate mechanical stress is calculated based on flow velocity and the geometrical characteristics of the trees and shrubs of species $s$ in height class $i$ by

$$H_{F,s,i} = \frac{C_d \cdot \rho \cdot v^2 \cdot A_{s,i}}{2} ,$$

where $v$ is the approach velocity for the plant (m/s), $A_{s,i}$ is the projected area of the plant of species $s$ in height class $i$ in the streamwise direction (m$^2$), $C_d$ is the drag coefficient of the plant, and $\rho$ is the fluid density (kg/m³). Flexible stems and varying

shapes of plants, particularly observed at pioneer softwood species, greatly complicate the determination of drag force, see Figure 7. Hence, the deformation of plant shape with flow precludes the use of a constant blockage area or the density of plant frontal area in predicting drag force.
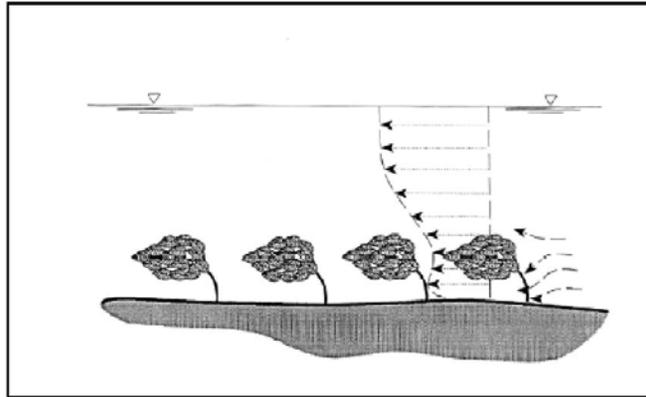


Figure 7: Reconfiguration of vegetation shape due to water flow
and influence of vertical flow velocity profile.

Via the drag force coefficient $C_d$, the drag force of rigid elements (in particular large stems) is calculated in this application through the theory of cylinders, whereas the drag force of flexible elements is calculated based the results of Freeman *et al.* (2000) determining the effective blockage area by taking into account reconfiguration of vegetation shape.

To note that via the vegetation-hydraulics interface the groundwater depth required for the soil water balance in RIFOD-W is determined, as well as maximal flow velocity to determine litter outwash in RIFOD-N and finally the daily wetted area and the maximal wetted area in the establishment module of RIFOD-P.

## C. MODEL INPUT

### C. 1 Climate and soil conditions for the ecological model

Climatic conditions, *i.e.* meteorological time series of precipitation as well as the parameters required for the PET calculation (*e.g.* daily atmospheric pressure, radiation) by the Penman-Monteith formula (1975), are not modelled explicitly due to the correlating properties of the meteorological parameters, but are based on data of meteorological stations. Data about soil profiles (number and width of horizons) and

soil texture (*e.g.* fraction of clay, sand) defined for each cell are read from an input file.

## C. 2 Topographical and hydraulic conditions for the hydraulic model

For the hydraulic model geometric data about the fluvial corridor, defined by the topographical height of each cell, are read by an input file, as well as the required daily discharge data.

## D. MODEL OUTPUT (ecological model)

Model output consists of the standard output of forest succession models, *e.g.* above-ground biomass (t/ha), or the number of individuals (Ind./ha) per tree and shrub species at the different height classes. This represents a large amount of information, which is visually impossible to analyze in detail. Therefore, we compressed this information by choosing a set of synthetic and ecologically relevant metrics as described below.

Based on the Shannon-Weaver index, representing evenness and richness of a vegetation community, Pielou's regularity index *R* [0,…,1] is calculated for all species together and separately for tree and shrub species by using

$$R = \frac{-\sum \left\{ \frac{Bio_s}{TBio_{ts/tt}} \cdot \ln \left( \frac{Bio_s}{TBio_{ts/tt}} \right) \right\}}{\ln S_{ms/mt}},$$

where $Bio_s$, is the biomass (t/ha) of a tree and shrub species *s*, $TBio_{ts/tt}$ the total biomass of shrub *ts* or tree species *tt* and $S_{ms/mt}$ denotes the maximal number of tree *mt* or shrub *ms* species on a patch. Note that maximum regularity (R=1) is attained if all species are present and have the same biomass.

To compare the composition between the different forest we use the percentage similarity coefficient (PS) (Bugmann, 1994), relating any two data sets $X = \{x_1, x_2, ..., x_n\}$ and $Y = \{y_1, y_2, ..., y_n\}$ by

$$PS = 1 - \frac{\sum_{i=1}^{n} |x_i - y_i|}{\sum_{i=1}^{n} (x_i + y_i)},$$

where $0 \leq PS \leq 1$ and $n$ corresponds to the number of tree and shrub species considered in the model. The PS determines the common fraction of values between two data sets and does offer the advantage not to track only differences in the relative distribution of the $x_i$ and the $y_i$ values (*e.g.* species-specific biomass) but it also declines the larger the difference between the sums of $x_i$ and $y_i$ (*e.g.* total biomass) becomes. Finally, based on the classification of Roulier (1998) – high woody vegetation (> 18 m, A), small woody vegetation (18 m> and > 8.0 m, a), high shrubby vegetation (8.0 m> and > 2.0 m, B) and small shrubby vegetation (2.0 m> and > 0.5 m, b) – the vertical height structure development is analyzed. Note that heights have been adapted in order to correspond to the limits of the height classes and that height class 0 is not included in the analysis.


# MODEL EVALUATION


Mankin *et al.* (1977) set as criterion for a valid model that all model behaviour must correspond to some real ecosystem behaviour. In this sense, Lexer and Hönninger (2001) pointed out that a forest vegetation dynamics model must be able to generate plausible species compositions along ecological gradients. Hence, they applied their model PICUS along a transect through the Eastern Alps in Austria. In floodplains ecological gradients (at least laterally) occur at a smaller scale (Gregory *et al.*, 1991). Hence, sensitivity analysis – considered as a validation procedure (Rykiel, 1996) – consists of an operational validation, a process sensitivity analysis and a parameter sensitivity analysis, performed by applying the RIFOD model to a hypothetical lateral profile for the River Rhone (section Central Alps, Valais); see Figure 8. In what follows the experimental set up, as well as the different elements of the sensitivity analysis are described in more detail.


## A. EXPERIMENTAL SETUP

Geometrical characteristics of the hypothetical fluvial corridor are as follows: total fluvial corridor width (200 m), minor river bed width (40 m), lateral major river bed slope (5 %) and longitudinal slope (0.0008 %); see also Figure 8. Daily discharge data (1981-2003) were available from a gaugig station in Branson (Switzerland), together with climatic data (1981-2002) of a nearby meteorological station. Yearly climate and discharge data series were randomly generated based on the available

data. Simulations started from bare ground including all 65 woody species. As regularly used to explain riparian vegetation zonation (*e.g.* Heller, 1969; Ellenberg, 1993), Figure 8 indicates also the over a period of 120 years calculated water level of an extreme flood (EF), of a mean flood (MF), as well as the mean water level during growing season (MVW), the annually mean water level (MWL) and the low water level (LWL) based on the available discharge data (including simulated vegetation roughness).
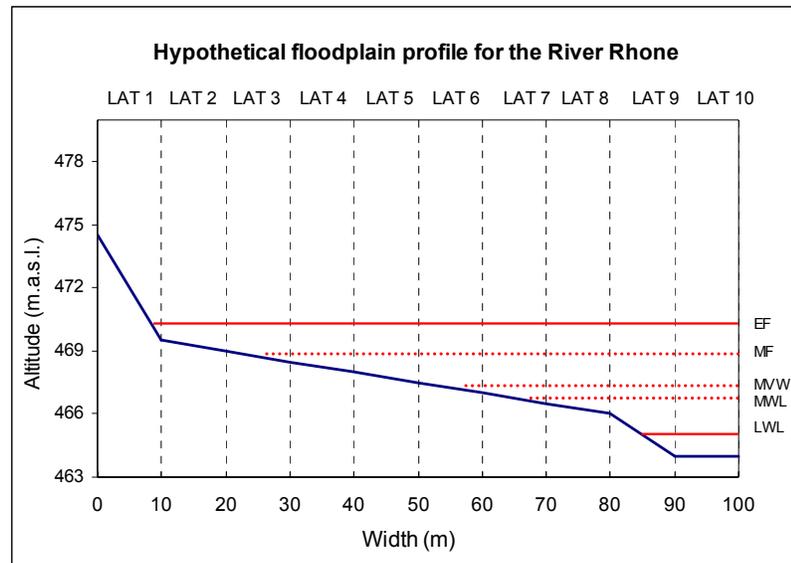


Figure 8: Hypothetical floodplain profile for the River Rhone with LAT 1-10 corresponding to the different lateral patches of the half-profile.

The high stochastic nature of the model, particularly due to hydraulic processes, needs a preliminary determination of the number of model repetitions required to reduce the variability of statistical parameters, such as the average, in view of comparing model results. Note that the averaged result does not necessarily correspond to the actual riparian forest composition in that area. The actual vegetation is the result of a specific history of climatic and hydraulic events and the resulting environmental conditions. Increasing the number of repetitions may improve statistical behaviour of the model, but would not imply an improvement of the reliability of the model results for a specific area. Figure 9 (a) and (b) represent the standard error of the mean (SE) of the total biomass (t/ha) and Figure 10 the coefficient of variation (CV) in function of the number of model repetitions for LAT 2 and LAT 6 at year 30. For LAT 2, SE is stabilizing after 30 model repetitions, as observed for LAT 1 to 5. In opposition, LAT 6 presents greater variations explained by particular flooding events and the small amount of individuals present on this

patch. The coefficient of variation displayed on Figure 10 highlights the greater variations of LAT 6 due to its more severe hydraulic conditions. Note that the RIFOD model simulated a successful establishment of tree and shrub species only for LAT 1 to LAT 6.

(a)

SE of total biomass (t/ha) in relation of model repetitions for LAT 2



(b)

SE of total biomass (t/ha) in relation of model repetitions for LAT 6
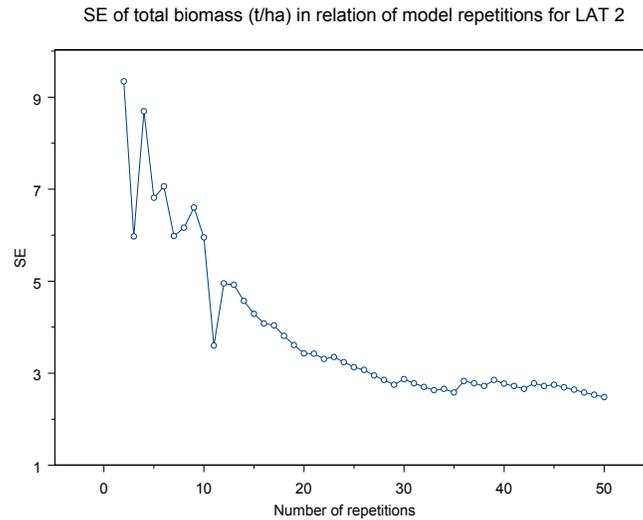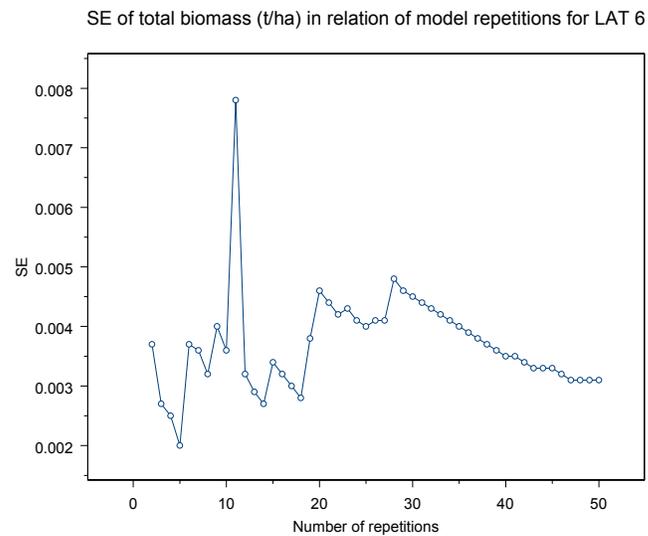


Figure 9: Development of standard error of the mean (SE) in relation of the number of model repetitions for LAT 2 (a) and LAT 6 (b) after 30 years of simulation.

CV of total biomass (t/ha)
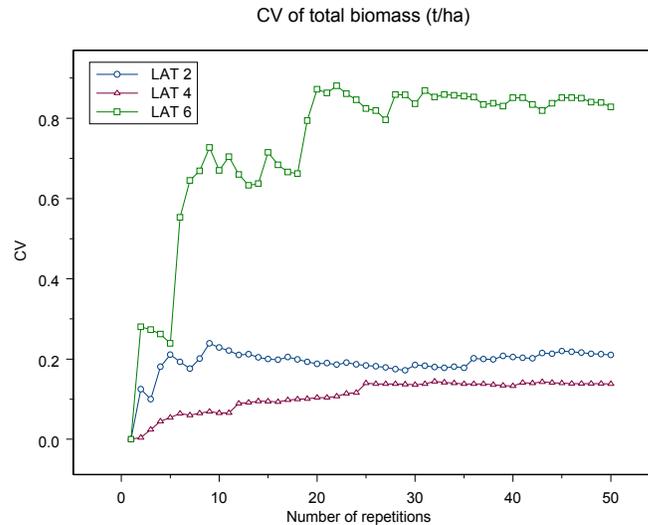


Figure 10: Development of the coefficient of variation (CV) in relation to the number of model repetitions for LAT 2, 4 and 6 after 30 years of simulation.

To illustrate the flooding characteristics of the different patches of the half-profile LAT 1 to LAT 10 Table 1 displays the averaged simulated values over a period of 120 years at 30 model repetitions. MFH corresponds to the averaged maximal flooding depth (m), FLD to the averaged flooding duration during the vegetation period (d), TLF the averaged time since last flooding (yrs), MWA the maximal wetted area and FDUR the fraction of the growing season where the maximal wetted area is reached. The table will be discussed within the process sensitivity analysis.

Table 1: Simulated flooding characteristics of the different patches LAT 1 to LAT 10 of the half-profile averaged over 120 years. Standard deviations are given in brackets.

|  | LAT 1 | LAT 2 | LAT 3 | LAT 4 | LAT 5 | LAT 6 | LAT 7 | LAT 8 | LAT 9 | LAT 10 |
|---|---|---|---|---|---|---|---|---|---|---|
| MFH (m) | 0.01 (0.07) | 0.04 (0.18) | 0.18 (0.27) | 0.54 (0.36) | 1.02 (0.38) | 1.52 (0.38) | 2.02 (0.38) | 2.52 (0.38) | 3.77 (0.38) | 4.77 (0.38) |
| FLD (d) | 0.00 (0.00) | 0.03 (0.23) | 5.69 (6.25) | 34.97 (21.25) | 87.41 (23.60) | 122.90 (15.28) | 152.24 (13.65) | 171.91 (7.95) | 180.00 (0.00) | 180.00 (0.00) |
| TLF (y) | 61.00 (34.96) | 24.59 (21.63) | 1.38 (0.75) | 1.00 (0.00) | 1.00 (0.00) | 1.00 (0.00) | 1.00 (0.00) | 1.00 (0.00) | 1.00 (0.00) | 1.00 (0.00) |
| MWA | 0.005 (0.03) | 0.05 (0.17) | 0.51 (0.40) | 0.92 (0.18) | 1.00 (0.00) | 1.00 (0.00) | 1.00 (0.00) | 1.00 (0.00) | 1.00 (0.00) | 1.00 (0.00) |
| FDUR | 1.34e-04 (8.65e-4) | 0.002 (0.003) | 0.004 (0.003) | 0.056 (0.05) | 0.260 (0.127) | 0.530 (0.13) | 0.717 (0.083) | 0.871 (0.067) | 0.967 (0.033) | 1.00 (0.000) |

# B. MODEL EVALUATION

## B.1 Operational validation

No quantitative field data relating long-term riparian forest composition dynamics to changing site conditions (due to hydraulic and geomorphological processes) exist at an appropriate scale to perform a data validation according to Rykiel (1996). However, data are not an infallible standard for judging model performance. Thus, an operational validation (*i.e.* whole model validation), testing how well the model mimics the system regardless of the mechanisms built into the model (Rykiel, 1996) is carried out. To do so, we consider as performance criteria the correspondence of the simulated riparian forest succession stages and composition to qualitative observations in the field. These include the qualitative riparian vegetation dynamics models of Roulier (1998). The author formulated specific qualitative phyto-sociological succession models for different riparian areas of national importance in Switzerland based on a synchronical approach, resulting finally in more generalized qualitative models illustrating typical riparian forest succession stages according to types of rivers systems and biogeographical areas. Even if these models do not allow a direct comparison in time and only to a limited extent in space, they allow deducing the plausibility of the simulated results concerning the appearance of dominant species in relation to the environmental conditions present. The simulation result of species specific biomass development (t/ha) over 120 years is compared to two qualitative models suggested for the riparian area Pfyn (Central Valais), the series of Polygonatum odorati-Alnocoenetum incanae typicum and the series of Melico nutantis-Pinocoenetum sylvestris. Former is found on sites more regularly flooded in opposition to the latter located generally on higher fluvial terraces. The series of Polygonatum odorati-Alnocoenetum incanae typicum correspond to the results simulated on LAT 3, whereas Melico nutantis-Pinocoenetum sylvestris to the ones of LAT 2, being in accordance to the site conditions in which these series were observed, as LAT 3 is more regularly disturbed by flooding (see Table 1). Figure 11 and 12 display the comparison of the simulated model results to the two qualitative models. For easier comparison, detailed phyto-sociological notations and characteristics were omitted and exemplary species were added to the qualitative model.

(a)
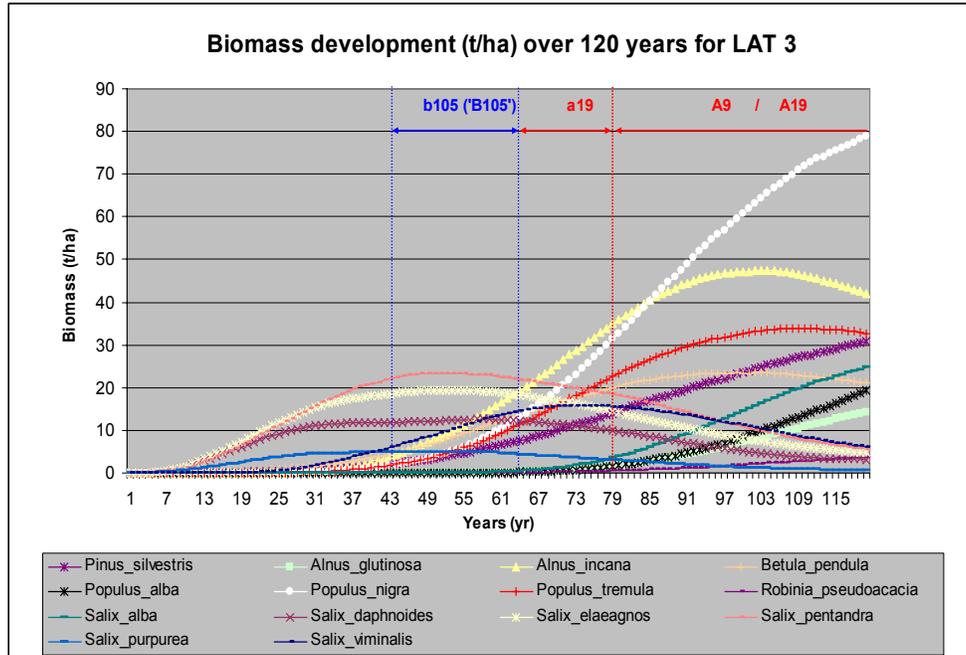


(b)
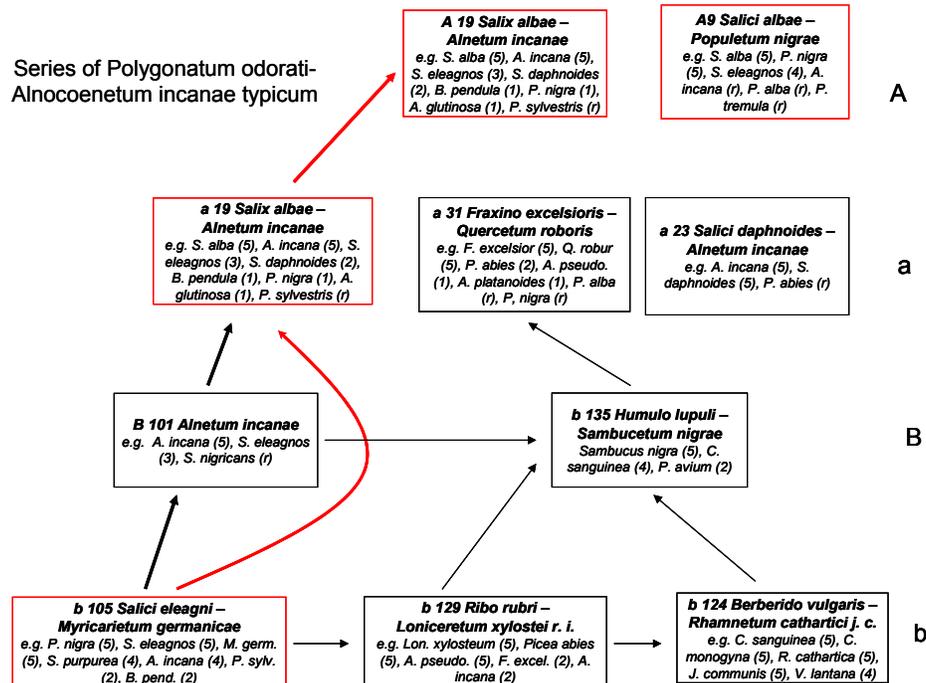


Figure 11: Comparison of RIFOD simulation result (a) to the qualitative succession model Polygonatum odorati-Alnocoenetum incanae typicum (b) of Roulier (1998) for the site in Pfyn (Central Valais).

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(a)
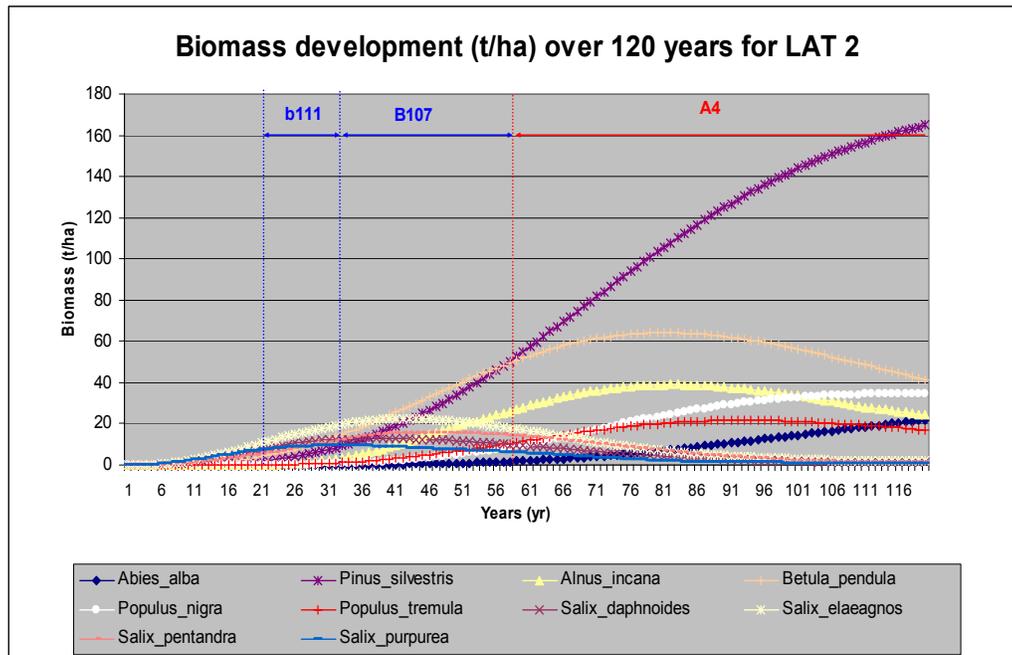


(b)
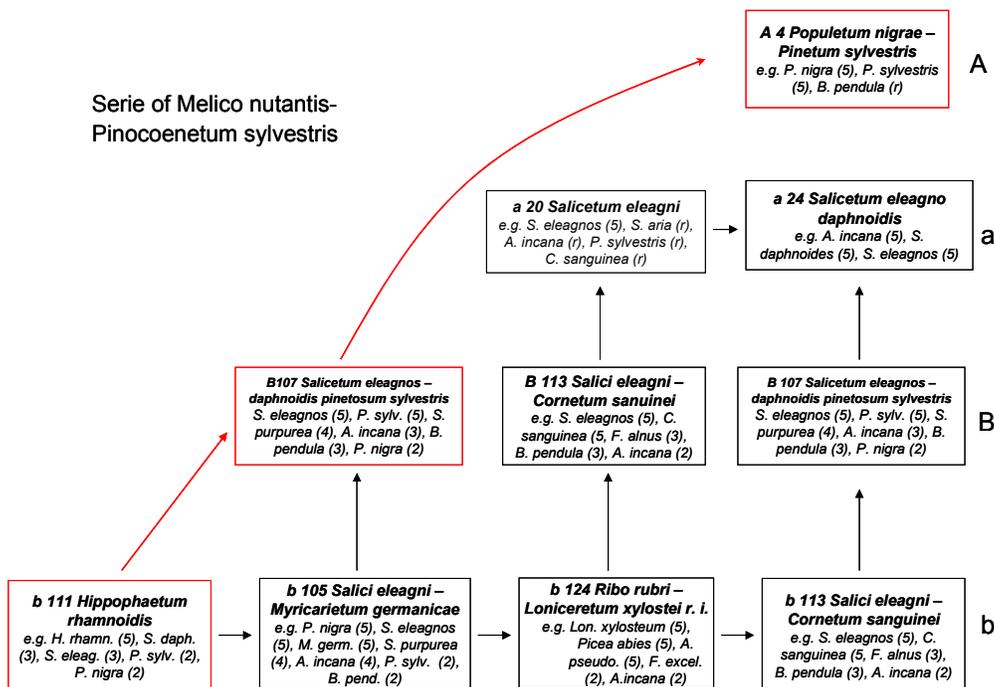


Figure 12: Comparison of RIFOD simulation results (a) to the qualitative succession model Melico nutantis-Pinocoenetum sylvestris (b) of Roulier (1998) for the site in Pfyn (Central Valais).

As mentioned, simulation results for LAT 3 are similar to the ones in Figure 11 (b); indicated succession step b105 → a19 → A19 / A9. The alliance of syntaxon b105 is characterized by a strong presence of *Salix eleagnos*, *Salix daphnoides* and *Myricaria germanica*, but also of *Salix purpurea*, *Populus nigra*, *Alnus incana* or *Pinus sylvestris*. Model results after about 40 years present the development of this syntaxon, which means the dominance of *Salix eleagnos*, the development of tree species like *Alnus incana* or *Pinus sylvestris*. However, b105 corresponds more to a B105, as it is preceded by a *Salix* stand having already reached a certain development stage. The alliance A9 and A19 cannot be separated in the simulation result as the associated species appear together. The series Melico nutantis-Pinocoenetum sylvestris, characterized by the dominance of *Pinus sylvestris* and *Populus nigra*, including the presence of *Alnus incana*, is similar to the succession step b111 → B107 → A4; see Figure 12 (b). The experimental set up chosen for the comparison resulted successfully in one of the different possibilities of riparian forest succession observed by Roulier (1998) for the Central Alps. The other succession variants within the two series may due to particular site conditions not covered by the chosen experimental set up. The main lack of synchronical approaches is that the formulation of succession series and their stages are not referenced in time. Therefore, further investigation, such as dendrochronological analysis would be required to determine the age of a stand associated to a certain succession stage. But even in this case, a direct comparison can not be done, as the real stand does not necessarily originate, as assumed, from bare ground (Bugmann, 2002).

## B.2 Process sensitivity

Process sensitivity is performed by comparing the averaged forest composition of RIFOD to different model variants presented in Table 2. The model variants were formulated based on ecological gradients observed in riparian areas and considered as important by many authors (*e.g.* Heller, 1969; Tabacchi *et al.,* 2000). This procedure allows to determine first, whether the importance of process is consistent with its ecological importance attributed in the field and second, to determine key parameters for integration in the parameter sensitivity analysis.

Table 2: RIFOD model variants used for process sensitivity analysis.

| Model variant | Environmental stress factors | | | |
|---|---|---|---|---|
| | Nitrogen scarcity | Drought stress | Flooding stress | Remarks |
| R-R | X | X | X | Standard model |
| R-U | X | X | − | Groundwater set at 2.50 m |
| R-N | − | X | X | |
| R-W | X | − | X | |
| R-F | X | X | − | |

The area plots shown in Figure 13 (pp. 119-121) illustrate the above-ground biomass productivity (t/ha) over a simulation period of 120 years for LAT 2, 4 and 6, for each of the considered model variants. In what follows, each of the considered model variants will be discussed separately.

Figure 13-1: Species-specific biomass dynamics (t/ha) versus years of simulation for LAT 2, 4 and 6 for the different model variants defined in Table 2 (30 repetitions).
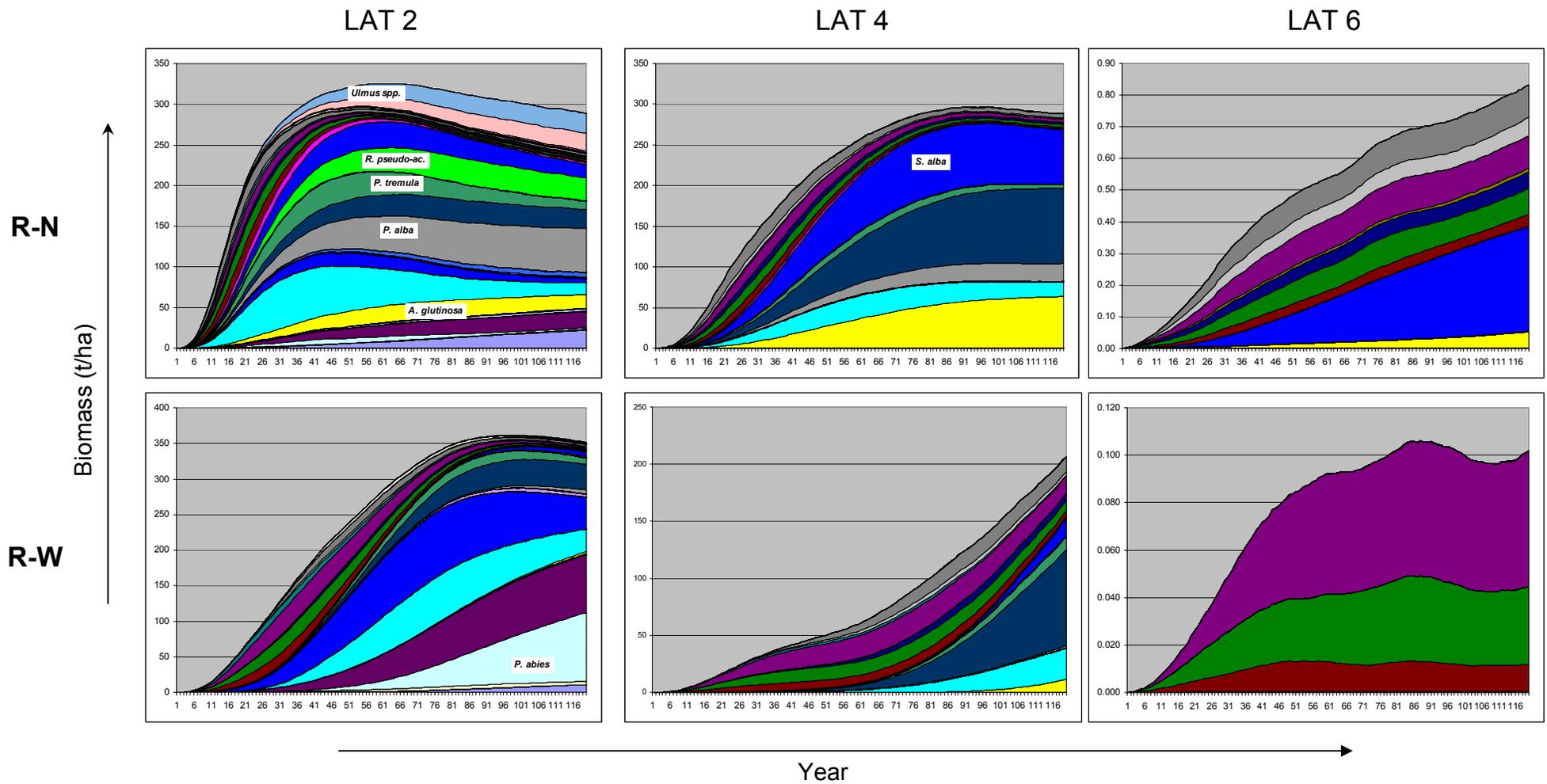
Figure 13-2: Species-specific biomass dynamics (t/ha) versus years of simulation for LAT 2, 4 and 6 for the different model variants defined in Table 2 (30 repetitions).
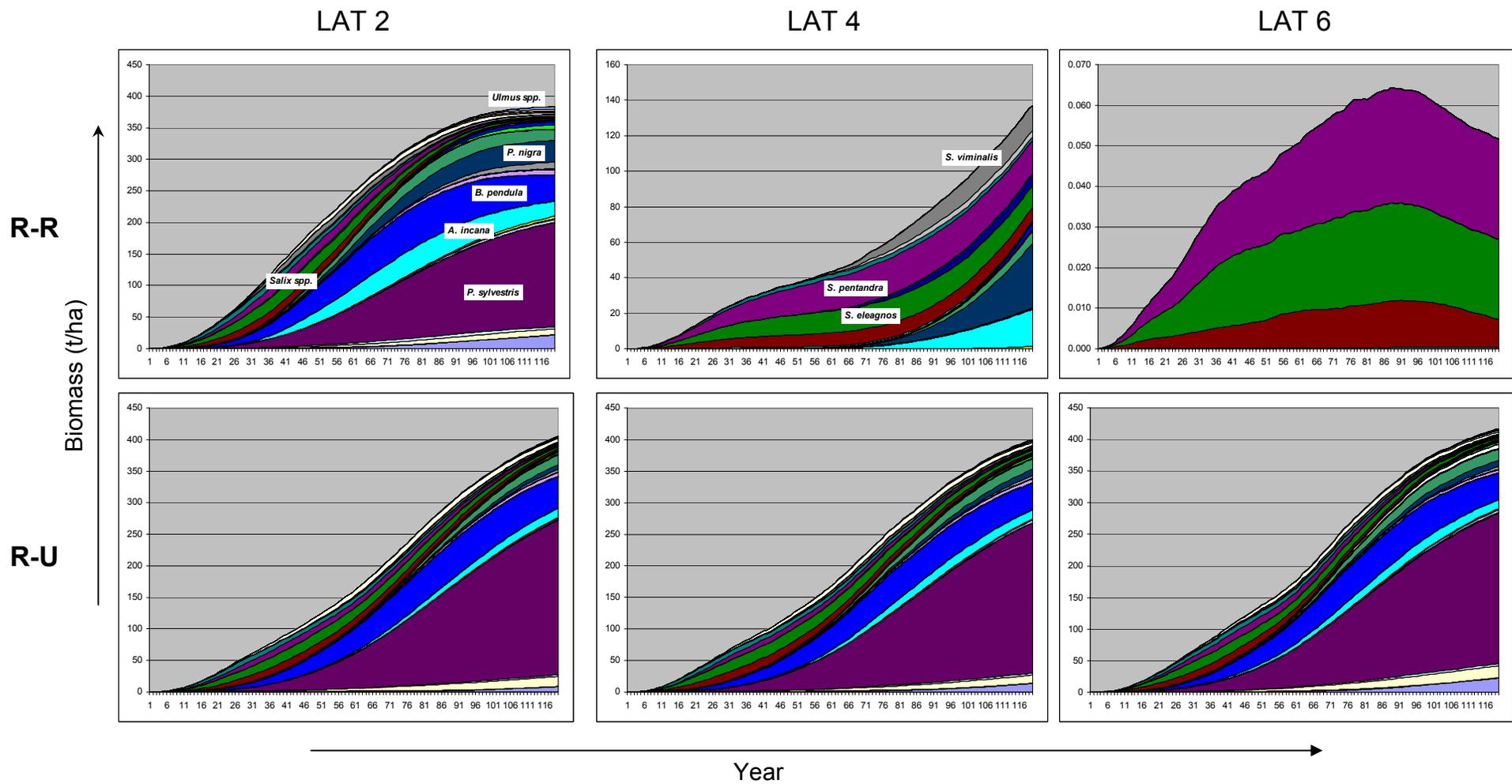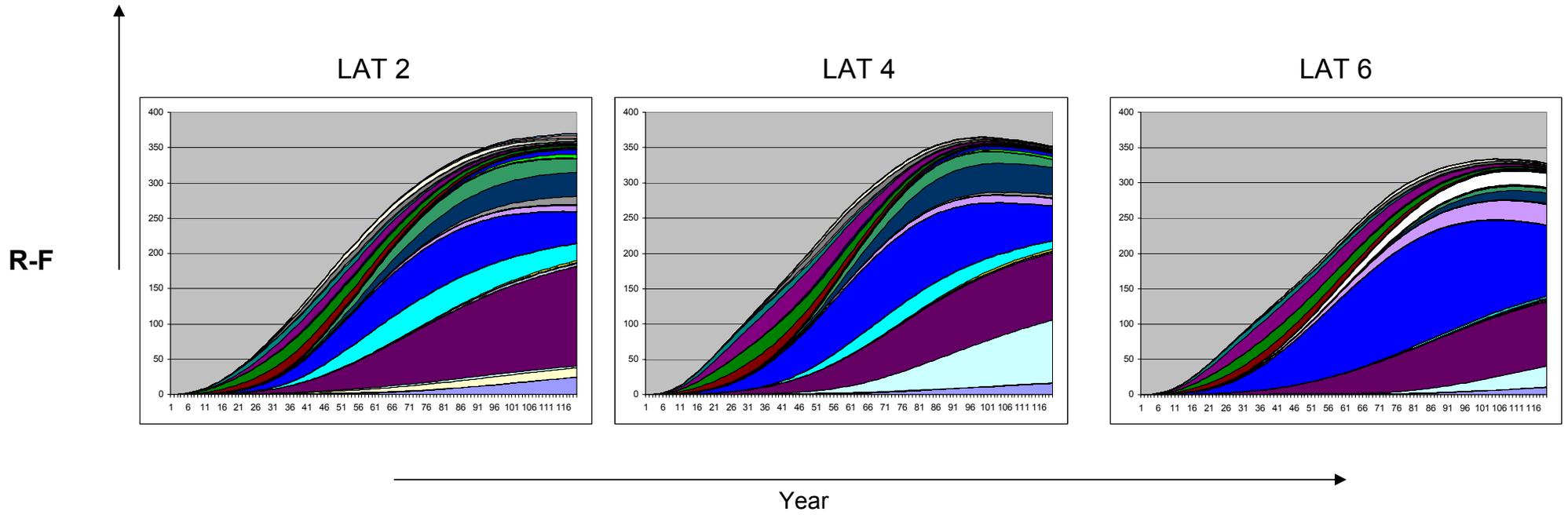
Figure 13-3: Species-specific biomass dynamics (t/ha) versus years of simulation for LAT 2, 4 and 6 for the different model variants defined in Table 2 (30 repetitions).

*R-R*

This variant shows riparian forest dynamics including all considered ecological and hydraulic processes. RIFOD simulates what has also been noted by Scott *et al.* (1997), namely that the early successional woody plants that dominate newly formed surfaces along streams typically demonstrate rapid growth, tolerance to nutrient scarcity, high seed production, such as *Salix eleagnos, Salix daphnoides* and *Salix purpurea*. Depending on the lateral position of a patch, riparian forest dynamics is the result of the interplay of the different gradients affecting it. In LAT 6 site conditions, particularly hydraulic conditions limit strongly species establishment and development. Thus only few *Salix* individuals can withstand this regularly mechanical and physiological stress; see Figure 14 (b). On the other hand, in LAT 4, the development of *Salix* spp. prepares the required site conditions (increased nitrogen availability) for the development of *Alnus incana* and *Populus nigra* according to the facilitation succession model (Connell and Slayter, 1977). Low disturbance by flooding, as well as more favourable soil moisture conditions (shallower groundwater level) result in a more rapid forest dynamics in LAT 2 compared to the upland variant. The enhanced dynamics in the first 50 years, as well as the total amount of standing above-ground biomass is in accordance with the observations of Pautou and Décamps (1985) and Naiman and Décamps (1997), which both point out the higher productivity of riparian areas ranging between with to 350-400 t/ha for a developed stand. As aforementioned, the limit of successful development of woody vegetation is at LAT 6, because of non-viable physiological and physical flooding conditions on LAT 7 to 10. According to Gill (1970) woody species cannot colonize a habitat when it is flooded for more than 40 % of the growing season, although it is possible that once established they may survive. Toner and Keddy (1997) come to a similar conclusion in their Canadian study which established a range of 36-38 % of the growing season as representing a barrier to seedling establishment, but less of a barrier to adult tree survival. Comparing these values with the result of Figure 14 (a) we can see that at a specific year, patch LAT 7 is completely flooded for more then 39 % of the growing season, whereas LAT 6 has a probability of ~15 % that it is flooded shorter than the establishment limit. Hence, LAT 6 presents periods in which woody species can establish, being in accordance with the threshold set by Toner and Keddy (1997). However, only few *Salix* individuals (> 1.30 m) resist the severe physiological and physical stress conditions of LAT 6, which is also illustrated by the strong fluctuations of individual numbers; see Figure 14 (b).

(a)
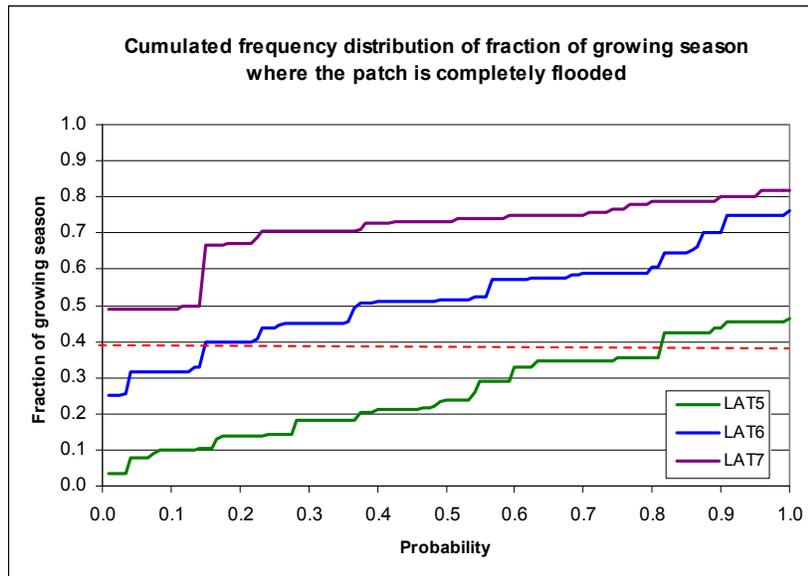


(b)
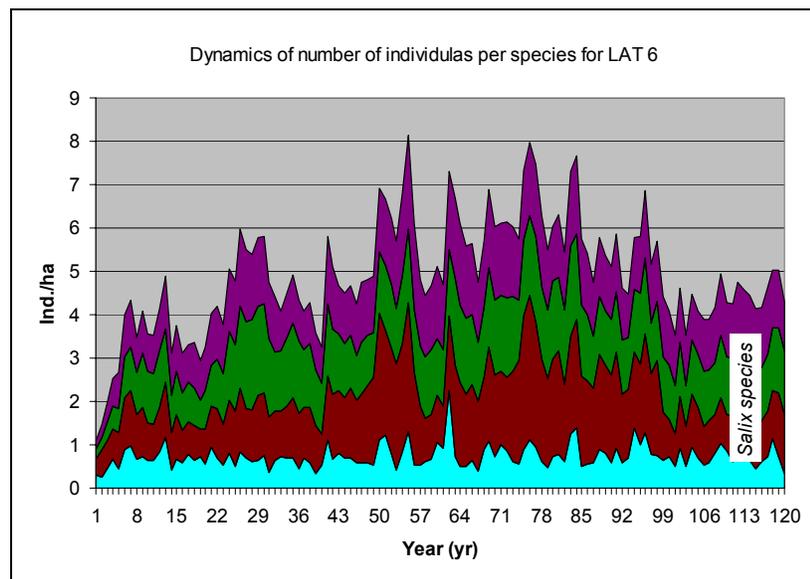


Figure 14: Model variant R-R. (a) Cumulated frequency distribution of fraction of growing season where the patch is completely flooded (establishment limit of 39 % indicated by dashed line); (b) dynamics of number of individuals (> 1.30 m) per species and per hectare of LAT 6 for a simulation period of 120 years.

Uprooting or stem breakage of trees and shrubs was limited to seedlings and saplings (results not shown), as observed by Gurnell *et al.* (2001) at the River

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Tagliamento. Therefore, as the results of R-R show no complete or partial clearance of the riparian forest (including extreme flooding events), we can state that drag force alone is not sufficient for reinitiating riparian forest succession, even in case of a high energy stream like the River Rhone. Hence, geomorphological processes as erosion (particularly lateral bank erosion) are of primer importance to destabilize adult individuals by reducing their uprooting resistance. Furthermore, the results underline the observations by Siegrist (1913) and Heller (1969), that in case of no geomorphological activity the mean water level (MWL; see Figure 8) during the growing season is more important then extreme flooding events (for alpine river systems). Indeed, they are of short duration and have, apart for seedlings, no radical impact on riparian forest dynamics.

Overall, the simulated vegetation zonation corresponds to the generalized vegetation zonation pattern of Central Alps suggested by Ellenberg (1996), with respect to the species found in the different zones as well as the associated flooding characteristics. For instance, on the regularly flooded patches LAT 6 (and LAT 5, not shown) typical softwood pioneer species (e.g. *Salix daphnoides*, *Salix eleagnos*) develop, representing the *Salix* belt observed at alpine rivers. The transition of the softwood to hardwood zone is characterized by the presence of *Alnus incana* or *Populus nigra* and finally the top hardwood zone (LAT 2), flooded only at extreme flooding events (EF; see Figure 8), by *Pinus sylvestris*.

*R-U*

Simulated forest dynamics of the upland scenario, which is very similar on all patches, underline that the different forest dynamics observed in R-R are the result of site conditions affected directly (flooding stress) or indirectly (*e.g.* groundwater level, nitrogen dynamics) by the river flow. Forest composition, dominated by *Betula pendula* and especially *Pinus sylvestris*, corresponds to the potential natural vegetation of the river adjacent areas of Pfyn. *Pinus sylvestris* is a pioneer species adapted to poor and dry soils, as well as to the continental climate prevailing in Central Valais.

*R-N*

Simulation results of model variant R-N are characterized by a highly accelerated dynamics, in which for LAT 2 maximal above-ground productivity is already reached after 50 years with early appearance of competitor species (Brzeziecki and Kienast, 1994) like *Ulmus* spp., being most successful on productive sites. Availability of nitrogen affects also total species diversity being after 120 years of simulation greatest on patches rarely disturbed by flooding, such as on LAT 2. On the more

regularly flooded patches (LAT 4 to 6), *Salix alba* and *Alnus glutinosa* find their ecological niche. This can not be observed as such at alpine rivers but rather on lowland rivers known to have better nutrient conditions due to finer sediments depositions including fine organic material (Carbiener and Schnitzler, 1990). In this sense, simulation results are in concordance with the observations of Heller (1969), Müller and Scharm (1996) and Gurnell *et al.* (2001), which outline the importance of nitrogen availability for the riparian forest dynamics in alpine river systems. Even pioneer *Salix* species, such as *Salix eleagnos* and *Salix daphnoides*, can have only a low secondary growth and reach only small heights due to the low nutrient availability (Müller and Scharm, 1996). In opposition to R-R, simulated lateral vegetation zonation for R-N corresponds more to the vegetation zonation pattern observed at European lowland rivers such as the Upper Rhine (Carbiener and Schnitzler, 1990; Michiels and Aldinger, 2002).

*R-W*

Simulations without drought stress reveal the appearance of *Picea abies* in LAT 2, known to be sensitive to limited water availability, the more *Salix alba* and *Alnus glutinosa*, both drought sensitive species, develop on LAT 4 in opposition to R-R. Compared to nutrient availability or flooding, water availability limitation has a visible smaller impact on plant development and forest composition. However, drought stress reduced above-ground biomass productivity on all patches, being in accordance to the observations made by Bayard and Schweingruber (1991), Johnson (1994), Patz *et al.* (2000) and Gurnell *et al.* (2001), which pointed out that in alluvial zones drought periods limit plant growth, particularly at the sapling stage. Ellenberg (1996) highlighted that for typical riparian species, drought may have even the greater impact as flooding. This is reflected by the simulation results for *Alnus glutinosa* and *Salix alba* on LAT 4.

*R-F*

RIFOD results corroborate observations by Ellenberg (1996) and others, that mechanical but especially physiological flooding stresses belong to the dominant processes for lateral vegetation zonation. However, their influences depend on the lateral position of a patch and the timing of the stress in respect of the development stage. In absence of flooding stress, tree species like *Picea abies,* known to require moist conditions, find on LAT 4 their fundamental niche due to the shallower groundwater level. In this sense, compared to the upland variant (R-U), the successful development of drought sensitive species, highlight the better soil moisture conditions of riparian areas as observed by Heller (1969) and others.

*Gradient analysis synthesis*

The aforementioned influence of the different gradients on the riparian forest dynamics can be comprising presented by the percent similarity coefficient (PS) of the riparian forest composition, calculated for each patch at year 30 and 120 using the species-specific biomasses (t/ha); see Figure 15. It is assumed that a PS < 0.8 indicates a sensitive process (Bugmann, 1994).

(a)
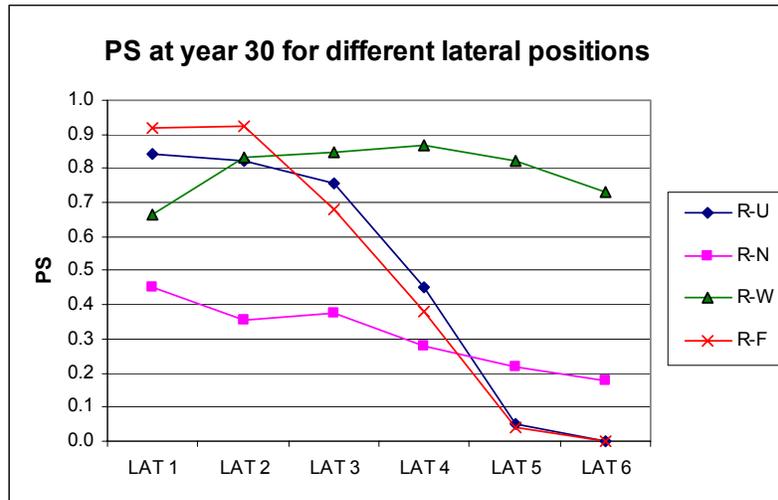


(b)
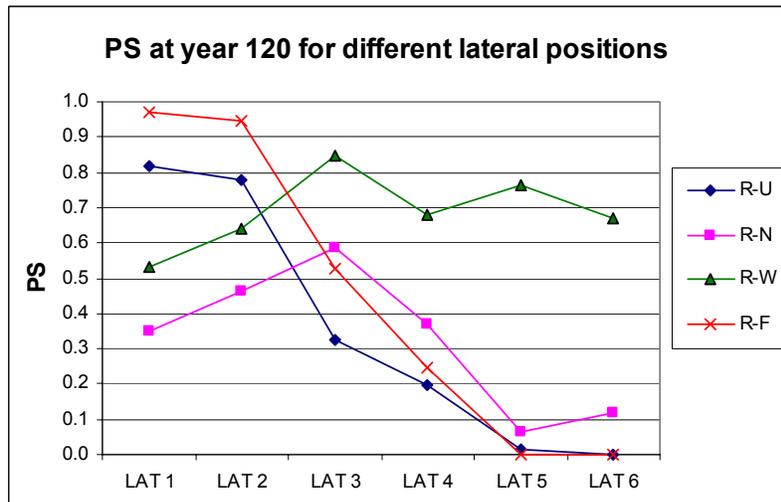


Figure 15: Comparison of the percent similarity coefficient (PS) for different model variants after (a) 30 and (b) 120 years of simulation (30 repetitions) using the species-specific biomasses (t/ha).

The PS values for R-N indicate, as seen before, that nitrogen availability affects strongly forest composition along the complete lateral transect but more on the patches flooded more regularly. This is typical to the situation found in alpine riparian areas with a low nitrogen input by deposits or river water. Moreover, this lateral gradient concerning the accumulation of organic matter and total nitrogen content is related to a decrease of perturbation by flooding and erosion (Heller, 1963; Amoros and Wade, 1993; Müller and Scharm, 1996). In case where not all of the patches are subject to regular flooding, this lateral gradient can be modified along the time axis; see Figure 15 (b). The balance between favourable moisture conditions and less flooding stress allows an accumulation of nitrogen on LAT 3 resulting in a higher PS value.

Overall, the PS results show that the influence of drought stress varies along the time axis and confirm, that it affects species composition (a) on river distant patches less influenced by flooding and with a deeper groundwater level, and (b) also at river near sites, such as on LAT 4 to 5; see Figure 15 (b), by affecting typical, drought-sensitive riparian species as mentioned before. The variability along the time axis is explained by the presence of deep rooting species with medium drought and high nutrient scarcity tolerance at the beginning of the succession. Nevertheless, the dominant process affecting plant development on the lateral transect is flooding. However, at the beginning of the succession nitrogen availability is limiting plant development on LAT 1 to 4 more severely than flooding, being aware the nitrogen dynamics is also related to flooding processes. Based on the process sensitivity analysis, we can hence state that the behaviour of the RIFOD model reflects the observed ecological processes of riparian forest ecosystems.

## B.3 Parameter sensitivity

Parameter sensitivity is concerned with the effects of large or small variations of species parameters on the performance of the model. According to Kräuchi (1994) models should respond realistically to changes in values of parameters and environmental conditions but should not be too sensitive so that realistic projections can be obtained without precise measurements of parameters. Based partially on the results of the process sensitivity, as well as on the sensitivity studies performed by Bugmann (1994) and others, parameter sensitivity analysis was focused on three key parameters: the growth scaling constant G, the nitrogen tolerance parameter Ntol and the submersion tolerance parameter Ftol. For the parameters denoting the tolerance of a species on a nominal scale in the range of [1,..,3] or [1,..,5], such as Ntol and Ftol, uncertainty was assumed to be $\pm 1$. For G, a relatively large range of

±30 % reflecting uncertainty was assigned (Bugmann, 1994). For the parameter modification a set of four species, namely *Populus nigra* (Ruderal strategy (str.); R)*, Juniperus communis* (Stress str.; S)*, Ulmus minor* (Competitor. str.; C)*, Pinus sylvestris* (C-R-S) has been selected following their abundance (two dominant, two non-dominant) and their life history strategy classification according to the CRS model of Grime (Brzeziecki and Kienast, 1994). In each simulation with the full species set only one of these parameters was changed. Parameter sensitivity is illustrated for the case of PS after 30 and 120 years of simulation using the species-specific biomasses (t/ha); see Figure 16. It is assumed that a PS < 0.8 indicates a sensitive parameter.

(a)
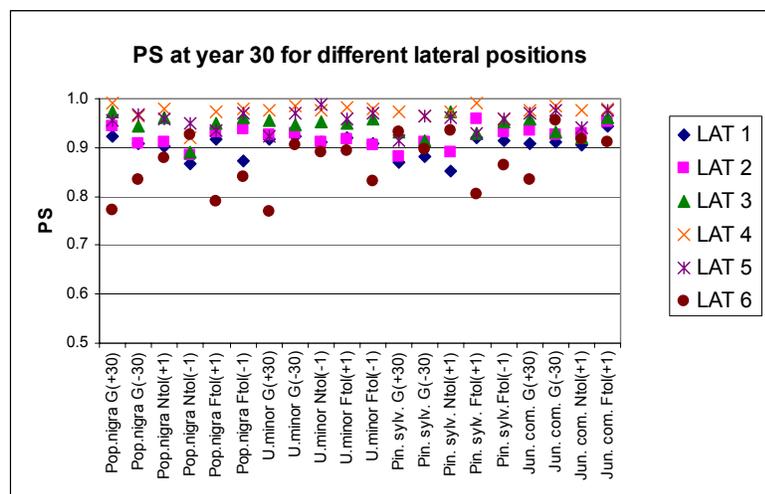


(b)
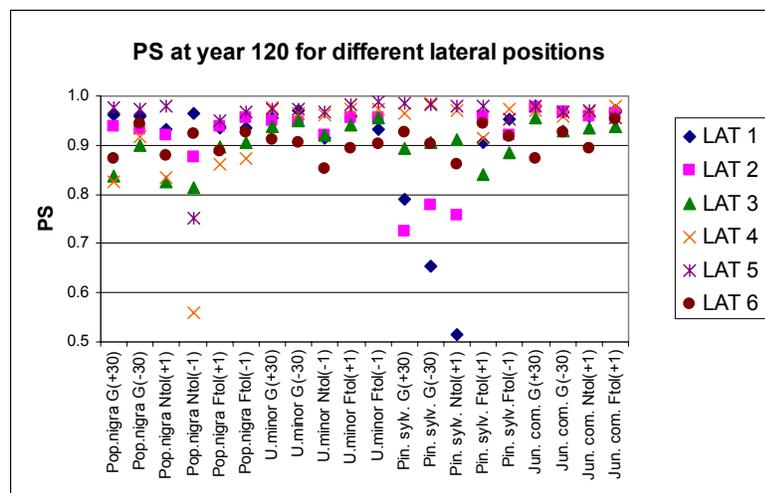


Figure 16: PS results for parameter sensitivity analysis at year 30 (a) and 120 (b) for species *Pinus sylvestris, Populus nigra, Juniperus communis and Ulmus minor* using the species-specific biomasses (t/ha).

At year 30, modifications of species parameter did not affect strongly forest composition as the PS values, except for LAT 6, are all greater than 0.8; see Figure 16 (a). The greater variability of LAT 6 is not due to parameter sensitivity but due to the stronger influence of the stochastic hydraulic processes; see Figure 10. At 120 years of simulation (Figure 16, b), forest composition did change for Ntol and G underlining their key functions; see for example Bugmann (1994). Parameter modification of dominant species, like *Pinus sylvestris* for LAT 1 and LAT 2, and *Populus nigra* for LAT 3 and 4, affect forest composition considerably in contrast to the less dominant *Juniperus communis* and *Ulmus minor*. In LAT 1 and 2 an increase of G increases the dominance of *Pinus sylvestris* affecting other species development by inter-specific competition. The opposite is valid for a decrease of the growth parameter (G-30 %) and of the tolerance to nitrogen scarcity (Ntol+1). Based on the sensitivity analysis we can formulate first, that the model parameter of Ntol and G can in some cases change forest composition considerably and this in the sense that the biomass of the most abundant species decreases strongly, however still remaining characteristic of the simulated forest. Second the relative sensitivity of the model varies along the time axis and along an ecological gradient in relation to the ecological niche of the species (the model responds more sensitively to changes in abundant species). Nevertheless, the set of dominating species produced by the default parameters seems to be rather robust to errors of parameter estimation, *i.e.* there are no species that turn up or disappear completely and alter the species composition qualitatively. However, as seen before, abundance of the species may vary markedly depending on the parameter values used. Thus, the simulated quantitative values of a given species, as well as the related indexes (*e.g.* regularity index), have to be interpreted cautiously.


## MODEL APPLICATION


RIFOD is applied, in view of opposing gain of ecological values to land use and to analyse model sensitivity to fluvial corridor geometry, to different lateral profiles corresponding to widening scenarios of the River Rhone in Valais (3rd Rhone Correction Project).


*Model boundary conditions*
As mentioned, the current version of RIFOD does not simulate geomorphological processes. Hence, the experimental setup integrates assumptions based on existing river widening practices which are (a) the lateral and longitudinal extension of the

minor river bed is dimensioned so that the river is in grade (*i.e.* regime river), which means in a dynamic quasi-equilibrium (Chang, 1988) concerning the geomorphological processes; (b) the minor river bed is stabilized by structural engineering measures blocking lateral erosion and by this lateral river migration for high energy streams as implemented at the River Thur (Switzerland) and projected for the River Rhone; and (c) a widening of the minor river bed goes ahead with a lowering and widening of the major river bed (floodplain). On the basis of these assumptions, RIFOD simulates for a specific section of the River Rhone (Riddes, Valais), the riparian forest dynamics for 12 different lateral profiles consisting of a minor river bed width of 90 m (= regime width), three major river bed widths of 50, 70 and 90 m (for one side) at four lateral major river bed slopes (0 %, 1 %, 2 % and 3 %). Figure 17 illustrates the four lateral half-profiles used for a major river bed width of 90 m in comparison with the actual half-profile of the River Rhone at Riddes (Valais).
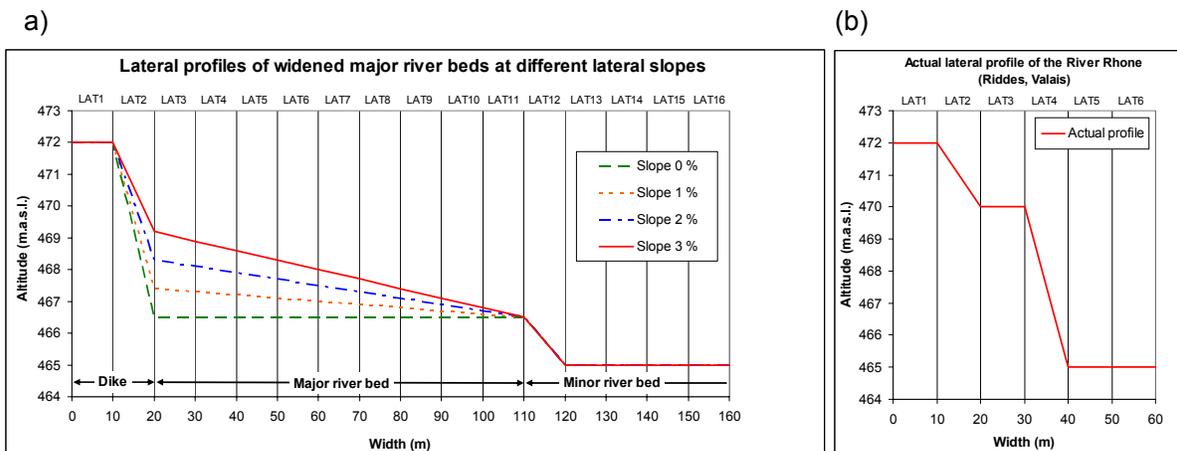


Figure 17: Lateral half-profiles of the River Rhone: (a) lateral half-profiles for the river widening variants at a major river bed width of 90 m, (b) actual half-lateral profile of the River Rhone at Riddes (Valais).

At present, woody vegetation developing on the dikes is regularly cleared in order to warrant their flood protection function due to a possible destabilization by rooting systems. Therefore, we do not assume a forest development on the dikes. A screening of the results is done after 120 years, where the maximal productivity at the river distant patches is reached. Next, for a given variant, the implications of a water regime modification on riparian forest dynamics is illustrated, *e.g.* by an installation of a hydroelectrical plant upstream a fluvial corridor widening.

*Determination of indicators for ecological values and land use*

Due to the previously mentioned uncertainty of the model and the compression of the model output, a qualitative expert evaluation of the ecological values of the riparian forest is performed based on following indicators: (a) the evenness of the forest composition (regularity index of Pielou); (b) the diversity of the vertical structure; (c) the relative above-ground biomass productivity; (d) the integrity of the riparian vegetation zonation (including non-vegetated surfaces); and (e) the width of the vegetated corridor in view of fulfilling landscape-ecological functions. For the above-ground biomass productivity (t/ha), the vertical structure (N° layers), the regularity index, the maximal values and their distribution pattern along the lateral transect are evaluated. For instance, for the vertical structure, the presence of patches with different combinations of vertical layers are favoured as in good vertical and lateral (horizontal) structured forests the supply of heat, light or water is higher than in poorly structured ones. Diverse structured forests increase the chance of a better habitat and site network for individual animal and plant species – the more as the offer more protection, cover and overview (Brändli, 2001). According to Stirling and Wilsey (2001) evenness is strongly correlated to species richness because higher species richness increases niche realization and subsequently evenness. Hence, the regularity index gives also insights into species richness of the lateral transect. Evenness values are compared at equal distances to the minor river bed. Next, in this application we regard the riparian vegetation zonation pattern as the most important indicator, as it integrates indirectly diversity of species (Frochot *et al.*, 2003) and diversity of processes. Thus, we assign a higher weight to this indicator (2x), which is evaluated by comparing the integrity of the simulated vegetation zonation to the riparian vegetation zonation of Ellenberg (1996) – favouring a gradually zonation to a short sequencing zonation. Habitat quality of the different zones is not only a question of composition but also of configuration, including space and vertical structure. Finally, to value also landscape-ecological functions, the width of the vegetated corridor was ranked. We assume that the wider the corridor the greater its ecological value. Forman and Godron (1986) identified width of the corridor as the most important feature for species composition. The ecological indicators are compared to a single land use indicator, which is the major river bed width. The ranking of the indicators is done following Simos (1990), by assigning to variants with similar ranking, an average ranking value. To illustrate model application, the indicators and their weights are defined for the 3rd Rhone Correction. However, the indicators would have to be formulated together with the stakeholders of the restoration project in an ordinary planning process.

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Figure 18 to 20 below display the lateral species-specific biomass, vertical height structure and the regularity index distribution at different major river bed widths and lateral slopes.
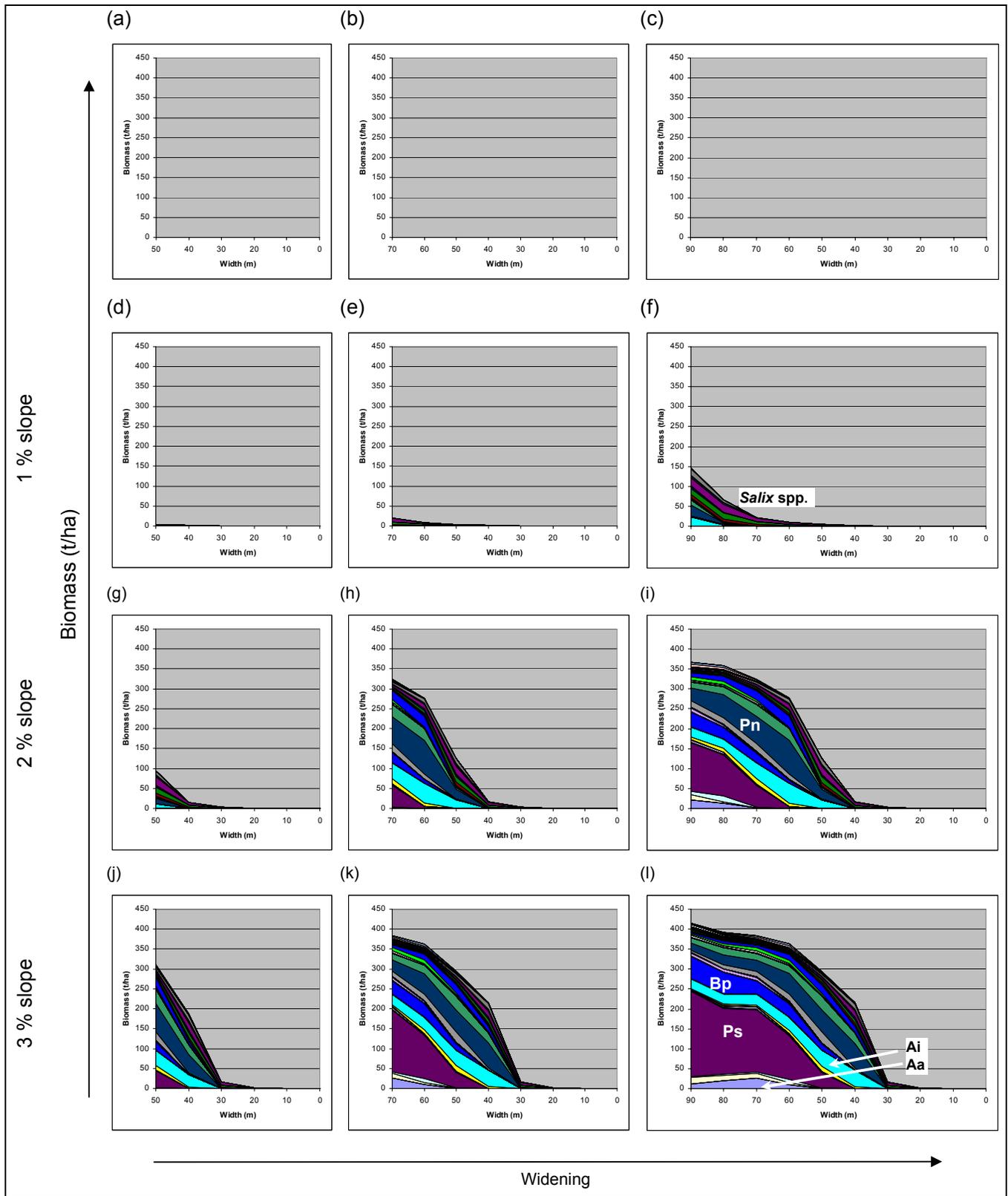
Figure 18: Lateral species-specific biomass distribution (t/ha) after 120 years of simulation at different major river bed widths (m) and lateral slopes (%). PS; *Pinus sylvestris*, Ai; *Alnus incana,* Aa; *Abies alba*; Bp; *Betula pendula*, Pn, *Populus nigra*, *Salix* spp. ; *Salix eleagnos*, *Salix daphnoides*.

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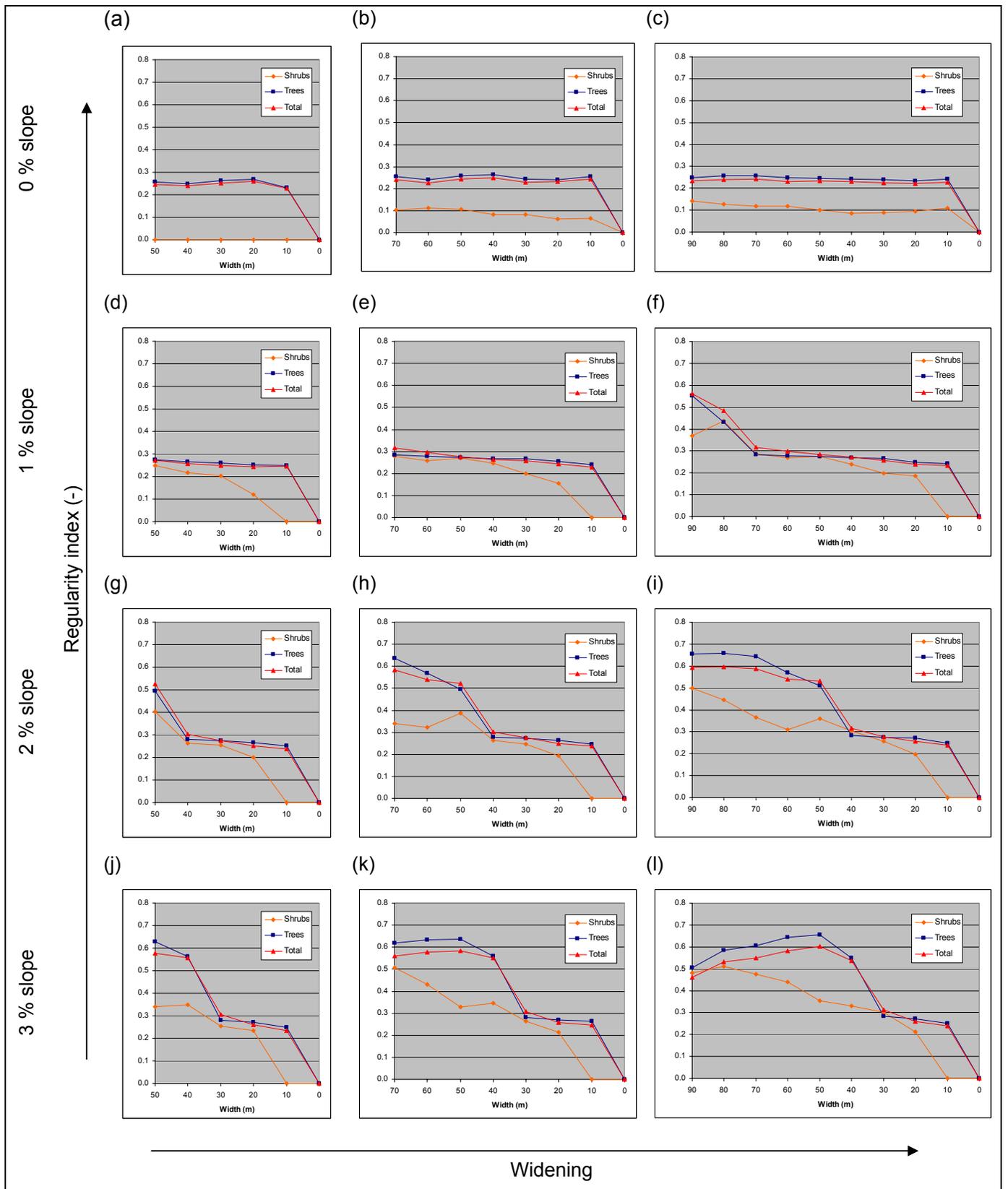
Figure 19: Lateral regularity index distribution for shrubs and trees after 120 years of simulation at different major river bed widths (m) and lateral slopes (%).
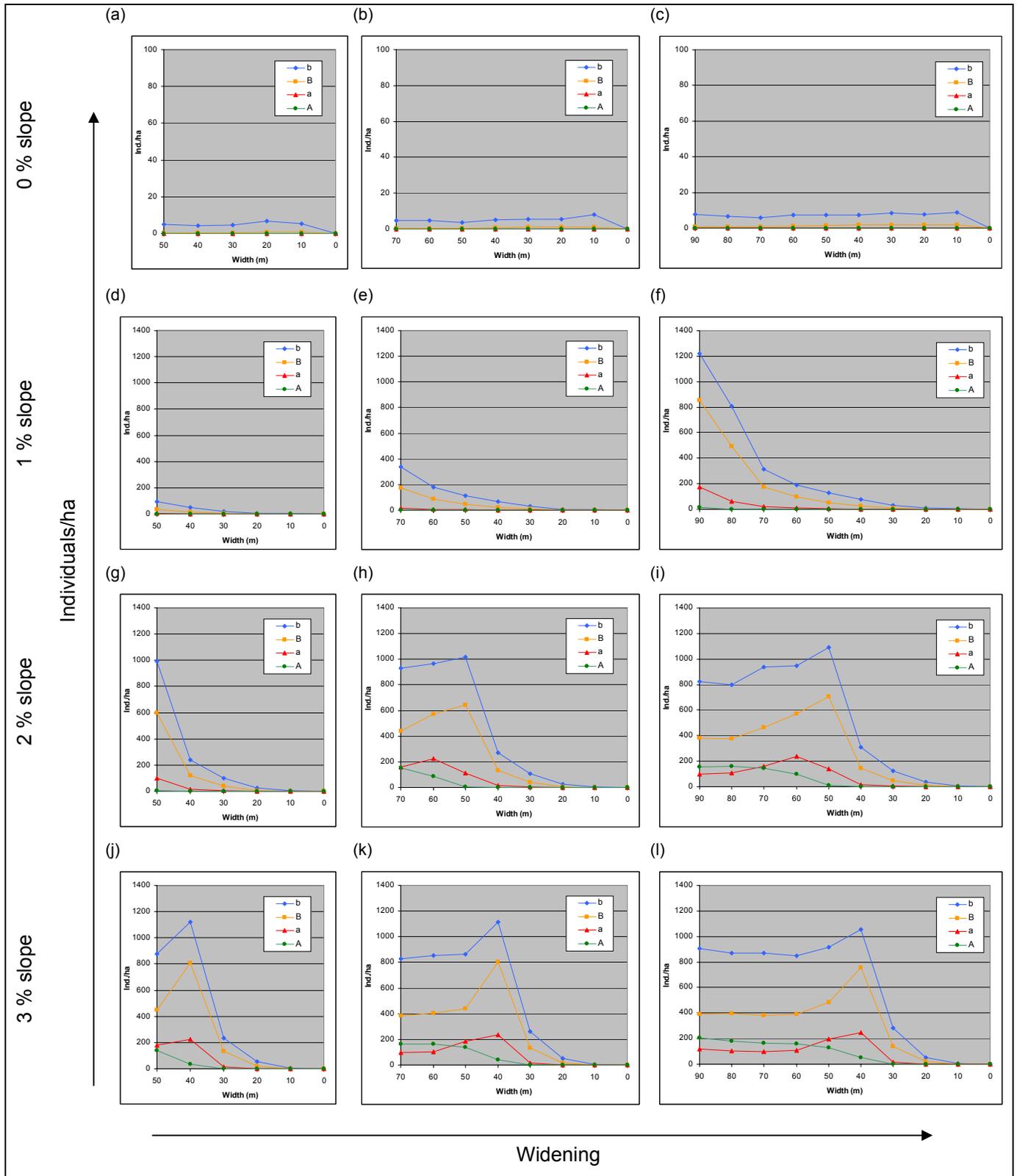
Figure 20: Lateral height structure distribution after 120 years of simulation at different major river bed widths (m) and lateral slopes (%). Lateral height structure distribution is expressed by number of individuals per hectare (Ind./ha) per layer (b; B; a; A).

At a lateral slope of 0 % only some individuals of *Salix* spp. establish, however at none of the major river bed widths they develop towards a structured and diverse riparian forest. Thus, the yearly water regime limits too severely plant development along the lateral transects. At a slope of 1 %, the above-ground biomass productivity increases, especially for a major river bed width of 90 m (Figure 18, f), at which on the river distant patches, the *Salix* spp. are succeeded by *Populus nigra* and *Alnus incana* due to improving nutrient conditions (accumulation of organic matter). Furthermore, a better height structure with three height structure classes can be observed (Figure 19, f). The appearance of additional abundant softwood species consequently increases the evenness at the river distant patches. With regard to forest composition, this result is qualitatively similar to the 2 %-variant at a width of 50 m; see Figure 18 (g). However, above-ground biomass is lower and the width of the vegetated corridor is smaller, reducing thereby the ecological value. At a slope of 2 % and a width of 70 m (Figure 18, h), productivity strongly increases with the presence of new softwood species, such as *Salix alba*, *Alnus glutinosa* or *Populus nigra*. Again, result similarities can be found between the aforementioned variant and the 3 %-variant per 50 m width (Figure 18, j), as well as between the 2 %-variant per 90 m width (Figure 18, i) and the 3 %-variant per 70 m width (Figure 18, k). However, the variants with the 2 % slope, present a wider and smoother transition from the shrubby *Salix* belt to the patches less exposed to flooding characterized by the dominance of *Pinus sylvestris*. This is underlined also by the appearance of new top hardwood zone species, such as *Abies alba* and *Picea abies*, which approach to 50 m the minor river bed at a 3 % slope (*i.e.* short sequencing zones), in opposition to 70 m at a 2 % slope. Next, with the gradual transition from one to four height classes a better lateral height structure distribution can be observed for the variant of 70 and 90 m at a slope of 2 % – in opposition to those of 3 %. The most productive variant, 3 % per 90 m, displays an increasing dominance of *Pinus sylvestris* at the river distant patches. This influences negatively evenness and thereby richness; see Figure 20 (l).

Table 3 displays the ranking of the indicators, as well as the qualitative, global rank of the simulation results in respect of ecological values and land use. The global rank corresponds to an average ranking of the ecological values and land use. The results are also displayed in Figure 21.

Table 3: Results of indicator's ranking in function of the different widening variants.

| Variant | | Forest characteristics | | | Riparian vegetation zonation | Landscape ecological effects | | | |
|---|---|---|---|---|---|---|---|---|---|
| Slope | Width | Productivity (t/ha) | Vertical structure (N° layers) | Evenness (Regularity index) | Pattern and sequence | Corridor width | Ecological values | Land use | Global Rank |
| 0 % | 50 m | 11.0 | 12.0 | 11.0 | 11.0 | 11.0 | 11.1 | 2.5 | 6.8 |
| | 70 m | 11.0 | 11.0 | 11.0 | 11.0 | 11.0 | 11.0 | 6.5 | 8.8 |
| | 90 m | 11.0 | 10.0 | 11.0 | 11.0 | 11.0 | 10.9 | 10.5 | 10.7 |
| 1 % | 50 m | 9.0 | 9.0 | 9.0 | 9.0 | 9.0 | 9.0 | 2.5 | 5.8 |
| | 70 m | 8.0 | 8.0 | 8.0 | 8.0 | 8.0 | 8.0 | 6.5 | 7.3 |
| | 90 m | 6.0 | 6.0 | 6.0 | 6.0 | 5.0 | 5.8 | 10.5 | 8.1 |
| 2 % | 50 m | 7.0 | 7.0 | 7.0 | 7.0 | 7.0 | 7.0 | 2.5 | 4.8 |
| | 70 m | 4.0 | 1.5 | 4.0 | 4.0 | 4.0 | 3.8 | 6.5 | 5.1 |
| | 90 m | 3.0 | 1.5 | 1.0 | 1.0 | 2.0 | 1.5 | 10.5 | 6.0 |
| 3 % | 50 m | 5.0 | 4.0 | 5.0 | 5.0 | 6.0 | 5.2 | 2.5 | 3.8 |
| | 70 m | 2.0 | 4.0 | 3.0 | 2.5 | 3.0 | 2.8 | 6.5 | 4.6 |
| | 90 m | 1.0 | 4.0 | 2.0 | 2.5 | 1.0 | 2.1 | 10.5 | 6.3 |
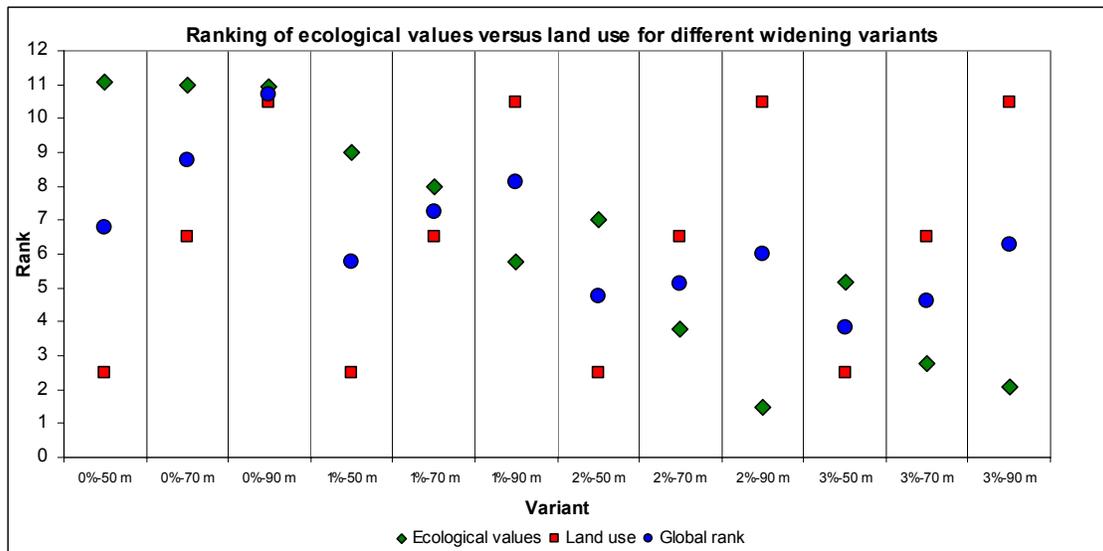


Figure 21: Ranking of ecological values versus land use for different widening variants, with the global rank as an averaged ranking of the ecological values and land use.

From an ecological point of view, the widening of 90 m at a 2 % slope is with a rank of 1.5 for the ecological values the best variant, whereas from the land use's point of view, this variant is not desirable. The worst variant is the one of 90 m at a 0 % slope.

It uses much terrain without being ecologically valuable in the sense of riparian forest dynamics. The best global rank has the variant at a 3 % slope and a 50 m major river bed width. However, it is followed directly by three other variants, 2 % - 50 m, 2 % - 70 m and 3 % - 70 m characterised by differing trade-offs between the ecological value and land use. Hence, the decision whether a widening variant is optimal or not depends on the objectives and the scope of a restoration project. It has to be considered that a strong modification of the water regime, *e.g.* by an installation of a hydroelectrical plant upstream a widening, can influence riparian forest dynamics and the associated ecological values strongly. Figure 22 illustrates the effect of a river discharge modification (daily water extraction of 150 m/s, minimal limit of river discharge of 50 m/s) after year 40, on the riparian forest dynamics at a distance of 50 m of the minor river bed (variant 2 % - 90 m).
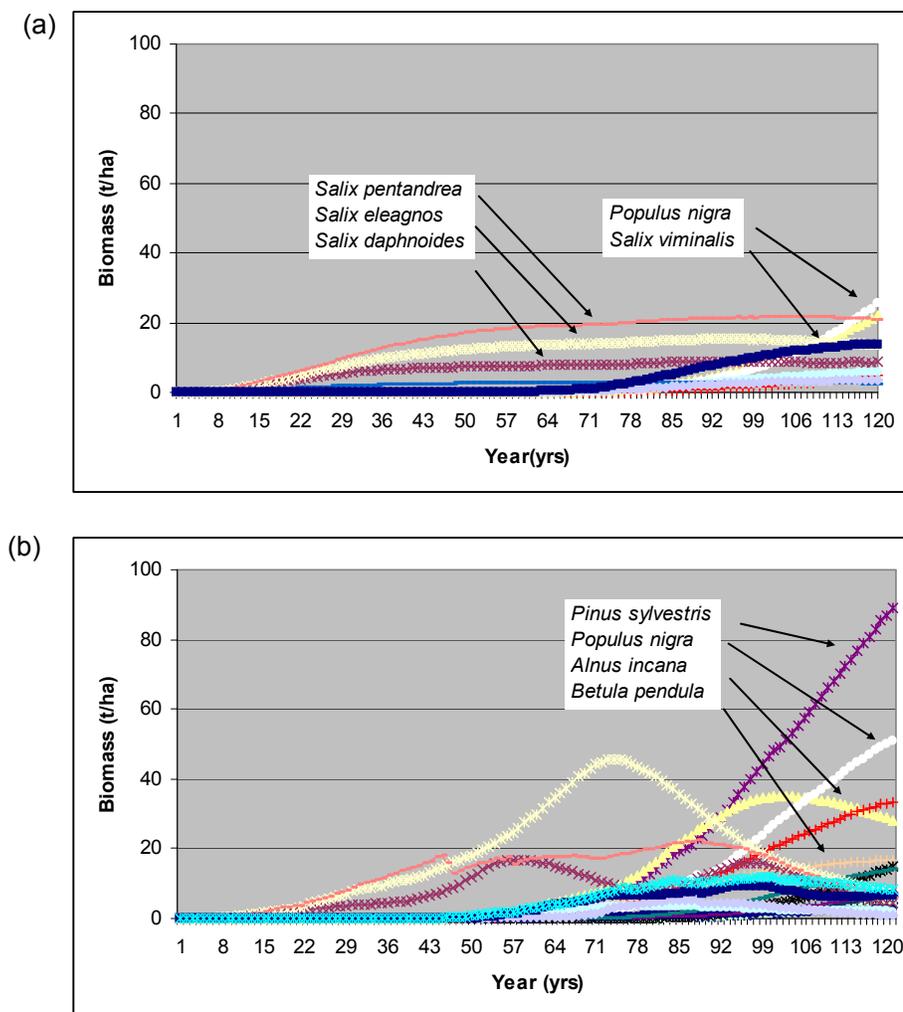


Figure 22: Riparian forest dynamics on a patch at a distance of 50 m the minor river bed (variant 2%/ 90m) for (a), non-modified water regime and (b) reduction of water regime due to an hydroelectric plant.

From Figure 22 we can observe that a modification of the water regime after year 40, the abundance of pioneer *Salix* species, particularly *Salix eleagnos* and *Salix daphnoides* increases for a short time due to a reduced flooding stress, but decreases after, as a result of the appearance of softwood species (*e.g. Alnus incana* and *Populus nigra*) but also of hardwood species (*e.g. Pinus sylvestris*) affecting the development of these *Salix* species by inter-specific competition. Overall, the riparian forest composition seems at a long-term to change to a more xeric forest composition.

# DISCUSSION

The following discussion is divided into three parts. Part A discusses the model structure, Part B the model evaluation, and Part C the model application.

## A. MODEL STRUCTURE

Up to now, forest succession models were mainly limit to model forest succession in upland areas and were primarily developed for application at a local scale, however not for specific locations but for virtual sites thought to be representative for a set of site conditions. Hence, they are not really suitable as decision support tool for specific locations. Furthermore, within the regional context they are often not spatially-explicit. However, the driving-processes (*e.g.* ecologic, hydraulic, geomorphologic) of riparian areas require a spatially-explicit modelling due to the strong interdependency of these processes. The RIFOD model is the first attempt to simulate spatially-explicitly riparian forest dynamics by a forest succession model integrating the different ecological processes occurring at a small scale, and to consider the interaction of vegetation and hydraulics by coupling the forest succession model to a hydraulic model. Compared to the model SWAMP (Phipps, 1979) and FORFLO (Pearlstine *et al.*, 1985), the novelties of RIFOD rely in the manner of modelling the ecological processes, such as regeneration but particularly the response of trees and shrubs to flooding, mechanical disturbance, drought and nitrogen scarcity. To do so, submodules of existing forest succession models (ForSum, Kräuchi, 1994; ForClim, Bugmann, 1994) as well as newly developed submodules (*e.g.* physiological flooding stress) have been coupled to the population dynamics model of TreeMig (Lischke *et al.*, 2005); see Figure 2. Within the model structure of the existing modules, general improvements were made at the process

level, and particular in regard of the conditions found in riparian areas. The large set of 65 Central European tree and shrub species parameterized allows a model application at a wide range of river systems and biogeographical areas within Central Europe.

*Population dynamics modelling*

The most important controls for a successful establishment of riparian trees by sexual reproduction are the lack of disturbance by flooding and the availability of moisture (*e.g.* Gurnell *et al.*, 2001; Johnson, 1994, 2000; Stromberg, 1993). This includes the timing of a flooding event within the dispersal and germination period determining germination success (van Splunder *et al.*, 1995). Compared to a flood at the beginning of the dispersal and germination period a later flood is more harmful. Indeed, the seeds (and young seedlings) are buried, washed away or die because of anoxia. On the other hand, seeds – particularly of softwood species – require a continuously moist substrate at least the first week of growth as they are highly vulnerable to drought. However at the end of the first growing season, their seedlings are able to survive strong declines of the groundwater level due to enhanced vertical root growth. Therefore the vulnerability of these plants to dry conditions decreases rapidly with age. The most of the forest succession models relate directly or indirectly germination success to soil moisture, for example by indicating the preference of a species for a certain soil texture or by relating germination success to groundwater level fluctuations. In opposition to FORFLO and SWAMP, RIFOD simulates the influence of ascending and descending water flows during the dispersal period on seed availability, the species-specific moisture requirements for germination and seedling development, as well as the flooding stress. Thus, the approach used in RIFOD combines the concept of the riparian recruitment box of Mahoney and Rood (1998) as well as the approach of Johnson (1994). The recruitment box defines a seasonal period for viable seedling establishment, when the timing of seed release coincides with an appropriate range of variation in stage and floodplain groundwater level range, and a rate of decline of the groundwater level that seedlings are capable of surviving (Richards *et al*., 2002). On the other hand, Johnson (1994) developed an index which combines the two factors, magnitude and regime, depicting recruitment potential. Ascending flows tend to remove fragile seedlings (by erosion or burial) recruited early in the period, whereas descending flows of the same mean tend to allow late period recruitment. To note that in the presented application of RIFOD, a more or less constant tree parent population in the neighbourhood for all 65 woody species was assumed. However, as a result of this assumption, riparian forest composition could theoretically be influenced in a manner not comparable to the field situation at a specific site (particularly if interest in short to medium-term forest

dynamics), as the species may not be abundant in the corresponding river adjacent areas. However, by modelling seed dispersal following the concept of TreeMig (Lischke *et al.*, 2005) or by qualitatively ranking species in the river adjacent area according to their abundance and adjusting by this seed input rates, this can easily be taken into account.

Asexual reproduction, including resprouting after loss of biomass, concerns the maintenance of the current generation, while sexual reproduction (*i.e.* seeding) concerns the production of future generations. In RIFOD we distinguished between root suckering, trunk sprouting and sprouting form transported plant fragments (*e.g.* rhizomes, branches). Bellingham and Sparrow (2000) noted that sprouting occurs in function of disturbance intensity and frequency, as well as site productivity. Hence, we related the process of root suckering to physiological flooding stress and trunk sprouting after death of a tree or shrub due to mechanical disturbance. Nevertheless, there is still great lack of empirical knowledge concerning processes of vegetative reproduction as well as the trade-offs between sprouting and seeding, particularly the definition of the switching points for different species.

*Physiological flooding stress response*
According to Glenz *et al.* (2005c; Chapter 4) a process-based species-specific modelling of flooding stress response based on physiological or metabolic processes cannot be done properly so far, as the relation between flooding stress and growth is still a field of investigation. Therefore, in attempt to use the broad but still vague knowledge about flooding stress, flooding stress response was modelled by implementing the fuzzy logic system suggested by Glenz *et al.* (2005c; Chapter 4) which covers the main abiotic factors affecting woody plant response to flooding. Furthermore, the use of flooding tolerance classes allowed considering implicitly the different metabolic, physiological and morphological adaptations of tree and shrub species and to by-pass the lack of species-specific data. In contrast to characteristic functions which defined hard thresholds in classical set theory (Adriaenssens *et al.*, 2004) as done in the approach of Phipps (1979) and Pearlstine *et al.* (1985), fuzzy membership functions allowed defining soft thresholds consistent with the ecological knowledge. Moreover, the processes can be represented transparently by the fuzzy logic system and because of this it can permanently be updated by new knowledge of qualitative (*e.g.* expert knowledge) or quantitative nature.

*Mechanical stress response*

So far, no existing forest patch model integrates disturbances by wind load or drag force including explicitly the responsible physical processes. The main reason can be found in their complexity, but also in the lack of species-specific data needed for calculating the different forces acting on the trees and shrubs, *e.g.* crown characteristics (height, width) and the rooting depths at specific development stages. In the model RIFOD, we adapted for the case of water flow existing mechanistic models simulating failure resistance to uprooting or bending based on experimentally and theoretically wind load studies. In relation to the development stage, the vertical rooting depths were calculated by the root growth model, whereas crown heights – used in the calculation of the mechanical stress as well as in the determination of the submersion level of trees – were estimated by a classification tree analysis. This analysis enabled us to integrate aspects of competition and site conditions of trees and to use the available categorical data. In opposition, most of the existing crown height models are statistical, non-linear models, relating the dependent variable to diameter or tree height. Some of them are already implemented in simulation software of forest growth models (*e.g.* BWINPRO; Nagel, 2001). However, the disadvantage of these approaches is that they imply that crown height is depending mainly on tree diameter and tree height following the dimension trend (*i.e.* bigger trees have automatically a higher crown) and that they ignore factors such as competition, stand characteristics or site conditions (Schmidt, 2001).

*Drought stress response*

In accordance to the observations in the field, RIFOD reflected that drought stress affects plant development not only in upland areas but also in riparian areas. Already Pearlstine *et al.* (1985) outlined that their model could benefit from considering drought stress by a drought stress function. By integrating and adapting the soil moisture submodule of FORSUM (Kräuchi, 1994) the model RIFOD can more explicitly model the soil water balance in order to determine drought stress at the germination and at the adult stage, as well as the required site conditions for the denitrification process. In opposition to the 'management by analogy' method used in FORSUM, by which physical behaviour of a soil horizons are expressed as a function of the properties of analogous soil layers, the use of pedotransferfunctions allowed a more realistic estimation of the soil hydraulic parameters of a specific site. Furthermore, these functions allow to more easily considering soil water retention capacity modifications in case of changing soil composition – in view of a future coupling of RIFOD to a geomorphological model. Similar comments hold for the integration of the vertical root growth model. It allowed: (a) calculating root water extraction in relation to the development stage of a stand, in opposition to FORSUM

where a species and development-independent homogenous root distribution was considered; and (b) determining species-specific and development dependent accessibility to groundwater in view of an improved drought stress modelling completed by the change of the root water extraction calculation and the consideration of the groundwater level. Groundwater – not considered in FORSUM – is an important element of the soil water balance in riparian areas and essential for the survival of particularly young tree and shrub individuals, as outlined by many authors.

*Nitrogen scarcity response*

The strong dynamics of quasi-natural riparian areas requires also a dynamic modelling of the nutrient status of a site, the more as the nutrient status substantially influences vegetation development in the uplands (Lexer and Hönninger, 2001; Bugmann, 1994) as well as in riparian areas. Dynamic modelling of the nutrient status, expressed by nitrogen availability, could be achieved by integrating and adapting the FORCLIM-S submodul of Bugmann (1994) to riparian conditions, particularly by considering the denitrifcation process. Denitrification belongs to the most important of nitrate loss in riparian areas. As the groundwater level raises due to flooding, the potential for anaerobiosis increases and consequently the potential for anaerobic nutrient cycling processes, which results finally in a loss of nitrogen (Baldwin and Mitchell, 2000). Due to the substantial influence of nitrogen availability on riparian forest dynamics, particularly at the beginning of the succession, a more detailed analysis and quantification of the nitrogen dynamics, its inputs (*e.g.* groundwater, river) or outputs (*e.g.* leaching) for specific riparian areas, as well as the impact of flooding on the nitrogen dynamics (*e.g.* importance of dry-wetting cycles) are required.

*Climatic conditions*

There exist many different methods at different time scales (hourly to monthly) to estimate PET – from simple empirical models to complex models, which are based on physical concepts. A simple empirical model at a monthly basis is the model of Thornthwaite and Mather (1957) requiring only monthly mean temperatures. It has been used in a wide variety of applications on both global and the local scale and has therefore found its way into forest succession models (*e.g.* ForSum, Kräuchi, 1994). Following Shuttleworth (1993) temperature-based evapo-transpiration estimation methods are not recommended unless this is the only available data source. In opposition to such an empirical model, the PET equation of Penman-Montheith (1975) is based on a sound conceptualization of the physical process of evapotranspiration of plant communities and is proved to be superior to a further 20

methods according to the results of a regression analysis of lysimeter measurements (Jensen *et al*., 1989). It is currently the most widely recommended and used method but requires more detailed measurements of driving variables, such as net radiation, windspeed, dewpoint temperature, air temperature, and vegetation-specific parameters. That's why the problem of the Penman-Montheith equation lies not in its adequacy but in the difficulty of applying it. However, in some countries the density of meteorological stations (*e.g.* Switzerland), and therefore also the availability of detailed meteorological data is increasing, hence the inclusion of more complex PET methods into forest succession models is possible. Particularly, as the integration of the Penman-Monteith method allows considering the plant-soil water-relationship feedback through the coupling of leaf area index and water use. Similar to other applications using the formulation of Penman-Monteith (Zierl, 2001), meteorological time series were not modeled explicitly due to the correlating properties of the meteorological parameters. To generate long-term time series of meteorological parameters and to consider these correlating properties new methods could be investigated such as general state-space models (GSSM). The GSSM, being very flexible models, have the advantage not to be restricted to linear and Gaussian assumptions. Therefore the fitted models are robust with respect to outlying observations and they are able to detect structural changes in the underlying process. Further they allow including climatic scenarios in the model (*e.g.* global warming).

*Hydraulic model structure*

The RIFOD model presented herein couples an ecological model with a hydraulic model. In the approach of Phipps (1979) and Pearlstine *et al.* (1985) riparian vegetation is seen as a purely dependent variable. Although floods may affect vegetation, they are also affected by it, owing to the contribution of vegetation to hydraulic roughness. Hence, in assessing the relationship between vegetation and floods, it is necessary to recognize that flood velocities at any point in the riparian area may substantially decrease as vegetation grows or abruptly increase if the vegetation is destroyed (Bendix and Hupp, 2000). The coupling of the forest succession model to the hydraulic model considers this. Moreover, the quasi steady-state, quasi-2D model approach allowed us emphasizing on the ecological relevant lateral dimension and to make the model spatially explicit in the sense of vegetation-hydraulics interaction. Furthermore, the calculation of the water flow at a daily time step, in opposition to the bi-monthly approach of Phipps (1979) and Pearlstine *et al.* (1985), allowed to more accurately model physiological and mechanical flooding stress and to meet the strongly varying water level of alpine river systems. A longer

time step would not have been coherent with the soil moisture model working at a daily time step.

## B. MODEL EVALUATION

RIFOD simulates plausibly the ecological gradients observed in the field and the resulting riparian forest dynamics in geomorphologically stable stream channels. Nevertheless, further validation procedures need to be done. Even if it may be useful to evaluate 'realism' and 'plausibility' of the model result, RIFOD was tested by a model-model comparison as the qualitative models are model constructs their self. Such a model-model comparison does not allow comparing quantitatively the species-specific proportions of biomass, number of individuals or other variables. This would be possible by a model-data comparison (Bugmann, 2002). Therefore, apart from the forest composition of dominant species, which seems to be rather robust to parameter uncertainty, species-specific absolute output values, *e.g.* biomass, number of individuals, as well as timing of the succession stages, are subject to considerable uncertainty compared to field data. Furthermore, availability of species-specific data was limited for some of the less known Central European tree and shrub species. Hence, the question which has to be raised is whether the model is credible in the sense of being sufficient confident to base scientific and management decisions on it. According to Rykiel (1996) credibility of a model is related to the amount of knowledge available, the purpose of the model and the consequences of any decision based on it. Increase of credibility can only be achieved by validating the current version of the model for river systems with different hydraulic regimes and site conditions. This can be done either by a model-model validation or preferentially by a model-data validation, consisting of a comparison of the model results to tree-ring chronologies or of long-term forest trials of geomorphologically undisturbed and unmanaged riparian forests. In Switzerland, this kind of data series was available neither for riparian areas of the River Rhone, nor for other quasi-natural or restored riparian areas.

## C. MODEL APPLICATION

The application of the current version of RIFOD is limited to riparian areas in which the geomorphological activity is not a dominant process *e.g.* lowland rivers. Consequently, in case of restoration projects, the model can only be applied to

widened fluvial corridors with geomorphologically stable stream channels (*e.g.* minor river bed is stabilized by hydraulic engineering structures).

*Model relevance for analysing scientific concepts and hypotheses*

From a scientific point of view, RIFOD allows us to understand pattern and processes in riparian areas that are too complex to explore by other methods and to study ecological concepts and hypotheses related to the riparian ecosystem or ecosystems in general, for example the concept of zonation and succession (a) or the intermediate disturbance hypothesis (b), both described below.

(a) According to Bendix and Hupp (2000), many authors find an explanation of riparian diversity in the intermediate disturbance hypothesis, which suggests that species diversity should be greatest where there are intermediate levels of disturbance. According to the intermediate disturbance hypothesis, intermediate magnitude and frequency of disturbance allow for the maintenance of multiple vegetation patches on sites with varying degrees of disruption and at varying successional stages. For the widening variant at 3 % per 90 m we could observe on river distant patches a decrease of evenness, and consequently richness (Stirling and Wilsey, 2001), due to the increasing dominance of *Pinus sylvestris* inhibiting other species development by resource competition. On the other hand, on the river near patches subjected to very severe flooding stress only some softwood species can develop. Thus, biological diversity is highest in-between these two stress levels (see Figure 16; I), which would confirm the intermediate stress hypothesis involving a trade-off between competitive dominant species which monopolise stable habitats and the few fugitive species that survive high levels of instability, resulting in a maximal diversity at intermediate levels of disturbance (Richards *et al.*, 2002).

(b) The appropriateness of applying successional concepts to riparian communities is contested by several authors. In contrast to the succession theory, zonation of species in a community is a spatial phenomenon while succession is a temporal process (Moor, 1958; Lugo *et al.*, 1990). For some authors the vegetation mosaic is guided mainly by textural and moisture gradients (linked to river dynamics) and by flooding frequency (linked to floodplain elevation and distance from the main channel). In this sense, riparian communities should be considered compositionally stable, maintained by periodic flooding, rather than successional, recovering from floods (Bendix and Hupp, 2000). Moor (1958) maintaining the zonation concept, points out that the plant communities on the river floodplain can also succeed in time, but that the substitution is induced by a change in habitat, either by sedimentation or

erosion. For the proponents of the succession concept for example, old softwoods are the result of extreme conditions that have disturbed the progress. The current version of RIFOD does not consider geomorphological activity (*e.g.* erosion, sedimentation) therefore it allows analysing these concepts apart of habitat change inducing substitution of a vegetation community. As vegetation dynamics start from bare ground, not previously occupied by a vegetation community, it is qualified as primary succession. Based on the simulation results we can observe that the three theoretical succession models (facilitation/tolerance/inhibition) suggested by Connell and Slayter (1977), explaining vegetation community changes, can be found together in a same riparian area. On the bare ground, nutrient scarcity tolerant *Salix* species develop modifying habitat conditions in favour of less tolerant species (*e.g. Alnus glutinosa*), according to the facilitation model. The facilitation model corresponds to the definition of genetic succession of Moor (1958). Alternatively, species install independently of the presence of first succession stage species. The change in dominance within a vegetation community is explained herein by the slower growth of the succeeding species (e.g. *Pinus sylvestris*) – corresponding to the theoretical tolerance model. Finally, the inhibition model, considering the species hindering the installation of others, is found at the final succession stages. These three models appear on different locations along the lateral gradient and at different periods along the time axis. Furthermore, the number of succession stages is dictated by the flooding conditions. For example, close to the minor river bed the development of *Salix eleagnos* and *Salix daphnoides* may facilitate the installation of species with similar flooding tolerances (*e.g. Alnus incana*, *Populus nigra*), whereas at river distant patches succession may continue by tolerance and inhibition succession ending by the installation of top hardwood species (*e.g. Picea abies, Fagus sylvatica*). Nevertheless, we can observe that a proximity to the minor river bed forest composition remains stable in form of a *Salix* belt. The severe flooding characteristics, as well as the low nitrogen availability, did not allow the succession by species of similar flooding tolerance ranges. Hence, these riparian communities are maintained compositionally stable by regular flooding – corresponding to the zonation concept. On more distant patches lower flooding disturbance allows the accumulation of organic material and consequently nitrogen. Therefore, the pioneer *Salix* species are succeeded by other species in the sense of an autogenic succession. Note that in absence of an initial nitrogen scarcity *Alnus* and *Populus* spp. would not require the facilitation by the *Salix* species and would establish directly. This would mean that there is no genetic succession and therefore we would consider it as zonation.

*Model relevance for analysing river management variants*

Taking into account the uncertainties and assumptions related to the model, RIFOD allows from a management point of view to visualize tendencies of riparian forest dynamics and the associated characteristics (*e.g.* forest composition, height structure) in respect of different widening variants and river flow modifications – either naturally or man-made. The simulated riparian forest dynamics at the River Rhone illustrates the relation of elevation and distance of a site to the minor river bed. Increasing the lateral slope suggests the compensation of width. Nevertheless, the steeper the lateral slopes the closer the low and top hardwood zones approach the minor river bed, resulting in a shorter zonation sequence affecting also ecological values. In the absence of geomorphological activity RIFOD illustrates that the hydraulic processes alone are not sufficient for reinitiating riparian forest succession, even for high energy streams such as the River Rhone. Lateral bank (*i.e.* channel migration) and surface erosion, removing vegetation from pre-existing surfaces as well as deposition of fresh alluvial surfaces, are essential processes required for the re-initiation of riparian forest dynamics and the associated mosaic of plant communities, as well as the attendant structural and species diversity. Moreover, geomorphological processes are also responsible for the removing of the organic layer (litter and humus), allowing the colonization of species that only germinate on bare mineral soil (Bendix and Hupp, 2000). Without re-initiation, heterogeneity will be reduced as each of the successional sequence will reach its ultimate stage. Thus, sylvicultural interventions will be required for maintaining a long-term structural diversity, functional heterogeneity and connectivity (Amoros and Wade, 1993). Next, the simulation results revealed that the ecological values, although increasing with the width of the fluvial corridor, follow a marginally decreasing curve (relative benefits become smaller as the width increases). However, not addressed in this study, similar shaped curves are also likely for the benefits from security and maintenance costs. In large river restoration projects, decision-makers compare different restoration variants integrating a multitude of objective-based criteria covering generally ecological, social-economical and flood protection aspects, as it is the case for the 3rd Rhone Correction Project. In our application we only gave an example of analysing the tradeoffs for different widening variants by integrating ecological – related to woody vegetation – and land use indicators using a simple indicator ranking method. However, for a coherent comparison of these different variants, criteria and indicators defined by the stakeholders of the project should be integrated in the evaluation procedure and their ranking procedure clearly defined, ideally by use of a multicriteria methodology for decision aiding. For example, ranking of ecological values would have been different in our application if the establishment of

top hardwood species (*e.g. Picea abies*) is not part of the ecological objectives – as top hardwood species may be already abundant in river adjacent areas.

With a hypothetical example of changing the hydrological regime (*e.g.* by installing a hydrolelectrical plant upstream the river widening) RIFOD could show the effects on riparian forest dynamics – turning into a more xeric forest. Such simulation results reflect what has been noted already by Hughes *et al.* (2000), pointing out that the increased river control generally reduces the opportunities for regeneration by pioneer softwood species. After channelization or interbasin transfers, hardwood forests encroached on areas which were previously occupied by *Salix* spp. Similar observations were made for example by Köstler *et al.* (1968). They noted that in case of a permanent decrease of the groundwater level due to river management investigations (*e.g.* lowering of discharges), tree species may lose accessibility to the groundwater level and will depend on their capacity to adapt to the fluctuation by elongating their roots or to use other water sources. Otherwise, species composition will change towards a more drought tolerant species composition (*e.g.* Siegrist, 1913; Hainard *et al.*, 1987; Richard and Lüscher, 1987).

*Outlook: Relevance of geomorphology-vegetation and geomorphology-hydraulics interactions in view of an application of RIFOD to quasi-natural rivers*
For the application of the current version of RIFOD, important assumptions were made in regard of the boundary conditions, *e.g.* stable lateral profile along the time axis. However, the lateral profile may change already by the accumulation of organic matter or at low sedimentation and erosion rates. Hence, riparian forest dynamics could be affected due to resulting modified flooding conditions. Nevertheless, the assumptions are plausible with regard to the existing practices in river management and river restoration. However, in view of an application of RIFOD to quasi-natural rivers with a dynamic river bed, the coupling to a geomorphological model is indispensable. The interactions between morphology and vegetation, as well as morphology and hydraulics could then be addressed. Morphologic effects on vegetation occur by sedimentation and erosion. When flow velocity drops as a consequence of increased vegetation roughness, transport capacity drops also and consequently sedimentation increases. This explains why particularly heavy vegetated zones are prone to sedimentation. Depending on the sediment layer depth it may act as a disturbance by burying the existing vegetation – an effect especially important for small and understory vegetation. Brookes *et al.* (2000) did assume in their study that only complete burial (*i.e.* sediment layer greater or equal to plant height) kills plants. Such sedimentation locations and those newly created by river channel migration represent potential colonization sites for pioneer softwood species

(*e.g. Salicaeca*). Hence, sediment texture, organic matter content and the plant seeds deposed with the sediments play an important role for subsequent ecological processes. In opposition, erosion – in combination with drag force – contributes to the partial or total uprooting of the vegetation in place, removes the organic rich topsoil as well as seeds, and changes the substrate texture. Brooks *et al.* (2000) considered simply that a plant is removed if erosion takes place to the depth of a proportion of the root depth figuring between 40-70 %. Finally, the role of vegetation in affecting erosion is complex and poorly understood. Vegetation generally reduces soil erodibility on the banks and on the floodplain, but its impact on bank stability may be either positive or negative. Vegetation plays an important role in reducing erosion by detachment and entrainment of individual grains or aggregates of bank material. Hence, compared to unvegetated banks or floodplains, erosion of well vegetated banks can be reduced by one or two orders of magnitude (Smith, 1976). The effects of flexible vegetation on morphology are characterized by a reduction of the velocities and shear stress experienced at the soil surface, primarily by shifting the virtual origin of the velocity profile away from the soil boundary, and secondarily by damping turbulence (Coppin and Richards, 1990). However, if velocities and stresses are sufficiently large, flexible vegetation becomes prone and its effectiveness in protecting from erosion is diminished. While trees do reduce mean velocities in the bank zone and on the floodplain, they may produce areas of accelerated flow and heavy turbulence associated with their wake zones resulting in local erosion (Freeman *et al.*, 2000). Methods to estimate the shear stress acting on the soil at the bottom of a vegetative channel lining can be found in Temple (1980). However, the required empirical parameter describing the potential of the cover to dissipate turbulent energy near the bed are only given for various grasses. Others use root tensile strength, areal density and root distortion during shear to estimate soil strength to evaluate streambank stability (*e.g.* Simon and Collison, 2002). So far, most of the investigations were done in relation of the effects of hydraulics on morphology, *e.g.* sediment transport from the channel to the floodplain. Simple models of overbank deposition using diffusion analogy have been developed for example by Pizzuto (1987).

## CONCLUSION

Herein we presented the development of RIFOD ('RIparian FOrest Dynamics') – a distribution-based forest succession model coupled to a quasi-2D hydraulic model – simulating short or long-term riparian forest dynamics at a yearly time step, conceived as decision-aiding tool in river restoration projects. The model, applied on

a 10 times 10 m mesh grid, is spatially-explicit concerning the interactions of the ecological and hydraulic processes and integrates 65 Central European tree and shrub species. RIFOD is based on developments of existing upland forest succession models, which at the process level were improved, adapted and completed according to the ecological gradients and processes observed in riparian areas (*e.g.* flooding, nutrients, moisture). Apart the coupling to a quasi-2D hydraulic model and the explicit modelling of the hydraulics-vegetation interactions, the principal novelties of RIFOD consist for example in the modelling of physiological flooding stress by use of a fuzzy logic system integrating the main abiotic factors affecting woody plant response to flooding. Moreover, the modelling of mechanical failure resistance to uprooting or bending by adapting existing mechanistic models conceived for wind load studies to the case of water flow, or the integration of a quasi-mechanistic vertical root growth model to more realistically simulate drought stress as well as uprooting resistance. The model RIFDO can simulate riparian forest dynamics in riparian areas in which geomorphologic activity is not a dominant driving-process *e.g.* lowland rivers or retention basins, and in case of restoration projects, to widened fluvial corridors with geomorphologically stable stream channels (*e.g.* minor river bed is stabilized by hydraulic engineering structures). Considering this, RIFOD simulates plausibly riparian forest dynamics as well as the ecological gradients observed in riparian areas. This at a variety of laterally and longitudinally defined profiles, as well as river flow modifications – either naturally or man-made. Despite the uncertainty of the models parameters and the complexity of the processes to be modelled, the value of the current model version relies in the capacity of indicating tendencies of riparian forest dynamics and associated characteristics in function of different fluvial corridor designs. Moreover, it allows a better understanding of processes and patterns in nature by allowing to explore the consequences of a set of explicitly stated assumptions that are too complex to be explored by other methods. Hence, it helps to provide a better theoretical understanding of riparian system's functioning. Further applications of the model to other river systems with different hydraulic regimes, the complementation of the actual modelling approach of ecological processes with new insights, as well as the substitution of the model-model validation by a data-model validation, will increase the model's reliability and credibility.

The model RIFOD is a step forward into a more integral modelling of the riparian forest dynamics and its processes in view of a decision-aiding tool for large river restoration projects. By integrating particularly geomorphological processes (including formation of islands), and processes related to large woody debris deposition, RIFOD could find its application also in quasi-natural rivers.

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# CHAPTER 7

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# General Conclusion

The main aim of this thesis was to develop a process-based, spatially-explicit riparian forest dynamics model for Central European conditions by integrating, improving and completing driving-processes of existing upland forest succession models according to the ecological gradients observed in riparian areas. Applied to different fluvial corridors widening designs the model should support and enhance the decision-making processes in river restoration projects and provide a better understanding of riparian forest dynamics.

The new model RIFOD, a distribution-based spatially-explicit forest dynamics model coupled to a quasi-2D hydraulic model, its development procedure, evaluation and application allowed:

- <u>integrating and testing</u> existing knowledge about the processes and relationships of riparian ecosystems. For instance, model development revealed that due to the complexity of interacting processes, the knowledge about flooding stress response of many Central European tree and shrub species is still sparse and, in some cases, contradictory. In the interest of simplicity, many of the field-studies carried out focused on the abiotic factors flooding duration and flooding depth neglecting the importance of other abiotic factors, such as flooding frequency/time since last flood or the chemical properties of the flood water. Moreover, no differentiation between the levels of submersion in relation to plant height (*e.g.* partial submersion) is made. We could also observe that apart from opportunistic studies, there has been no long-term monitoring of individual species response on quasi-natural rivers sites. However, such long-term studies would be essential not only to add and to improve existing knowledge, but also to develop a useful method for estimating the impact of flooding on species development. The same holds for combining laboratory experiments, mostly carried out on seedlings, with field experiments. Apart from flooding stress response, model development revealed also the lack of species-specific knowledge about vertical rooting dynamics (mechanisms) of Central European tree and shrub species. Most of the quantitative data available are punctual observations of rooting depths in

relation to specific soil types and species age. However, as already for flooding stress, continuous record of the environmental conditions during vertical root growth would be required for a better theoretical understanding and hence an ecophysiological modelling approach. Knowledge gaps could also be found concerning the regeneration processes, for example the responsible factors for the trade-off between sexual and asexual reproduction or the impact of flooding on the nitrogen dynamics. Overall, we can state that there are still great gaps in understanding the detailed functioning and interaction of the responsible driving-processes for the riparian forest dynamics, as well their spatio-temporal variation. Most of the available knowledge of processes and species response is of qualitative nature, limiting an ecophysiological implementation into a modelling approach. Moreover, the lack of quantitative data in respect of riparian forest dynamics and site conditions makes a data validation of the model difficult.

- <u>providing</u> a unifying conceptual framework for thinking about the interplay between the various driving-processes that govern the system, followed by the implementation of this conceptual framework into a theoretical system.

- <u>modifying</u> freely the theoretical system, to incorporate alternative (known and/or hypothesized) mechanisms into the model and to investigate different restoration alternatives. This flexibility allowed the evaluation of known concepts or hypotheses (*e.g.* intermediate disturbance hypothesis) regarding the responsible ecological mechanisms, predicting the spatio-temporal dynamics of the system or the variables of interest and determining the impact of different fluvial corridor designs and management decisions (*e.g.* modification of discharge). In opposition to the adaptive management strategy for example, the behaviour of the system can be predicted without manipulating the real system, *e.g.* riparian system, itself.

- <u>visualizing and quantifying</u> the impact of the assumptions made being important for the decision-making process.

Based on the aforementioned points, modelling of spatially-explicit riparian forest dynamics can be a very interesting tool in river restoration and riparian system analysis. However, related to parameters and to the to-be modelled processes, every modelling approach contains uncertainties, as the best model is only the real system itself. Hence, models still trade off generality against precision and try to formulate the system's key processes and parameters adequately, in order to minimize these

uncertainties. Nevertheless, even if modelling is not a magic bullet, the value of the developed model RIFOD relies clearly in the capacity of displaying plausible tendencies of riparian forest dynamics and the associated characteristics in function of different fluvial corridor design variants. Moreover, it allows the understanding of processes and patterns in nature by allowing exploring the consequences of a set of explicitly stated assumptions that are too complex to explore by other methods.


# OUTLOOK

The model RIFOD, as models in general, can continuously be improved, either at the structural, the evaluation or the model application level. The main focus at the structural level of RIFOD should be put on integrating morphological processes in view of an application to quasi-natural river conditions. Furthermore, the actual empirical and semi-empirical implementations of RIFOD (*e.g.* crown width modelling) should steadily evolve to a more ecophysiological modelling approach, in order to more reliably 'apply' the model to new situations. Apart from structural and functional adaptations, another focus should be put on increasing model's reliability by applying the current model version to other river systems with different hydraulic regimes, and by substituting the model-model validation by a data-model validation of the sub-modules as well as of the entire model.

At the actual stage of development RIFOD is mainly of academic interest. However, a credible, user-friendly riparian forest ecosystem model could increase cost-efficacy of the river restoration planning by enhancing the decision-making processes and, in contrast to the adaptive management approaches, by avoiding regular cost-expensive modifications of the engineering measures. Visualization of the riparian forest dynamics *e.g.* by GIS or graphical interfaces would facilitate the application of the model by non-expert users.

# APPENDIX

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## Parameters of European tree and shrub species and their derivation

As far as possible, species parameters of the model TreeMig (Lischke *et al.*, 2005) and ForClim (Bugmann, 1994) have been taken on and completed for the additional tree and shrub species.


### *s-Type/B, s-Type/N and s-Type/H*

The s-Type/B parameter separates evergreen from deciduous species, as they differ in the specific leaf area and the dry to wet weight ratio of foliage. In ForClim (Bugmann, 1994) the values for s-Type/N parameter, describing the relationship between diameter at breast height and foliage weight of the corresponding species, were derived based on a large data set covering eight species which are *Abies alba, Picea abies, Pinus silvestris, Pinus cembra, Pinus montana, Larix decidua, Fagus sylvatica, Quercus* spp. in Burger (1945-1953). Based on these data five relationships were defined in ForClim. The remaining species – for which no data were available – were assigned to one of these relationships based on their capability to cast shade (described by Ellenberg (1996, p. 119)) and the values of the parameters A1 and A2 used in the FORECE model (Kienast, 1987). For RIFOD, the additional 35 woody species were also assigned to one of these relationships based on the indications of Ellenberg (1996) or by analogy. For example, all *Salix* species are supposed to have the same relationship as *Salix alba* in ForClim. As *Juniperus communis* is also an evergreen species it was assigned to class 5. The shrub species were all assigned to class 1, in regard of the shrub species *Alnus viridis* which was also assigned to 1 in ForClim.

The definition of the parameter s-Type/H, indicating species habit type, is particularly difficult for *Salix* species as some of them develop either as a shrub or as a tree, depending on the environmental conditions. In RIFOD, assignment of the habit type for *Salix* species is based on Schiechtl (1992). *Ilex aquifolium* is considered as a tree, whereas *Juniperus communis* is considered as a shrub.

### $D_{max}$, $H_{max}$, $A_{max}$

Parameterization of species concerning the maximum diameter at breast height ($D_{max}$), the maximum height ($H_{max}$) and the maximum age ($A_{max}$) is based again on ForClim. For the additional tree and shrub species a large data base was compiled for deriving the three aforementioned parameters from the silvics descriptions in Amann (1954), Prentice and Helmisaari (1991), Becker (1982), Godet (1986), Bartels (1993), Bernatzky (1978), Rameau *et al.* (1989), Aymonin and Timbal (1986), Kruessmann (1979), Ammann and Petra (1997), Schiechtl (1992), and particularly Geyer (1997). From every data source, the maximum diameter at breast height, the maximum height and the maximum age were recorded for each species listed. Following Bugmann (1994) the arithmetic mean of all values may not reflect true maximum dimensions since some authors probably were not aware of very large specimen. On the other hand, using the maximum of all the values would introduce a strong bias towards exaggerated large dimensions. Hence, in RIFOD the same method as in ForClim has been used, by calculating the average of the mean and the maximum values of the additional woody species. To note that for most of these species few data were available. In ForClim no parameter for *Alnus viridis* could be derived at all. Since this species is a bush rather than a tree, Bugmann (1994) set $D_{max}$ to 20 cm. In RIFOD, $D_{max}$ was also set to 20 cm for shrub species for which no data could be collected. Nevertheless, for *Prunus domestica* the maximum diameter was estimated based on the values of other *Prunus* species, like *Prunus avium* and *Prunus padus*. As some *Salix* species develop either as shrub or as tree species, maximum height and maximum diameter would need to be adapted following their habit.

### Gr parameter

For most of tree and shrub species no indications of maximal diameter increment could be collected. Hence, the maximal diameter increments required for Equation (1) were approximated based on Geyer (1997), indicating the age at which 80 % of the maximal height is reached using an exponential relationship, and based on the assumption that between age and diameter an exponential relationship exists. By means of the growth equation of Moore (1989) and assuming a linear relationship between diameter and height, the necessary regression coefficient for the age-diameter relationship was determined. Considering that maximal diameter increments occur mostly at early development stages, the assumption of a linear relationship can be justified. Overall, even if the absolute values of $Gr$ may not be completely reliable, the aim of the approach was to receive a correct ranking of the species with respect to their $Gr$ parameters as competitive success is based mainly

on the relative ranking of species with respect to a certain parameter (Bugmann, 1994). Nevertheless, the values are in the range of those of Kräuchi (1994), but higher compared to the values of Bugmann (1994).

Once the maximal diameter increment estimated, the growth parameter constant $Gr_s$ (cm/yr) for species $s$ was calculated based on the adapted equation of Bugmann (1994) given by

$$Gr_s = \frac{dD_{max}}{a_s} \cdot \frac{H_{max,s}}{D_{max,s}} \quad \text{and} \quad (1)$$

$$a_s = a_{max} \cdot \frac{H_{max_s}}{H_{max_s} + K_{s,a}},$$

where $H_{max,s}$ is the maximum height of a tree or shrub of species $s$ (cm), $dD_{max,s}$ denotes the maximum diameter increment at breast height (cm) and $D_{max,s}$ is the maximum diameter at breast height (cm) ($a_{max}$ = 0.1465 and $K_{s,a}$= 538.27).

Geyer (1997) did not indicate the age-height relationship for every species. Hence, a $Gr$ value has been attributed to the missing species based on species values of the same genus or growth type.

*DrTol (1 = non-tolerant, 5 = tolerant)*
Parameter derivation for drought tolerance was mainly based on the humidity indicator of Ellenberg (1996), but also on the humidity indicator of Landolt (1977). However, the parameters have partially been adapted in the case where qualitative descriptions (*e.g.* Ehlers, 1960) revealed clearly different tolerances.

*NTol (1 = tolerant, 3 = non tolerant)*
Species-specific tolerance values of nitrogen availability limitations (nitrogen scarcity) were compiled from Landolt (1977), Ellenberg (1996), Prentice and Helmisaari (1991) and Jahn (1991). The NTol parameters were derived from these sources by averaging and rounding to the nearest integer number. However, for some species the NTol values have been adapted following qualitative indications of Ehlers (1960) and others. For example following Ehlers (1960), Lange and Lecher (1993), *Populus tremula* prefers nutrient rich soils, whereas *Alnus incana* can also develop on nutrient

scarce sites, therefore a higher NTol value has been assigned to *Populus tremula* and a lower to *Alnus incana*. Finally, NTol values for *Juniperus communis* and *Crataegus monogyna* are entirely based on qualitative indications.

**lighs/ligha** *(1 = shade tolerant, 9 = shade intolerant)*
This parameter was derived based on indications of Ellenberg (1996) and Landolt (1977), for example for *Aesculus hippocastanum* and *Prunus domestica*. Qualitative data were also integrated (*e.g.* Ehlers, 1960).

**Lq** *(1 = fast decay, 2 = medium decay, 3 = recalcitrant)*
Based on Ellenberg (1996), *Ulmus* spp., *Alnus glutinosa*, *Fraxinus excelsior*, *Robinia pseudo-acacia*, *Prunus padus*, *Carpinus betulus*, *Castanea sativa* were considered as producing fast decomposing litter (C/N < 30), *Acer pseudoplatanus*, *Tilia* spp., *Quercus* spp., *Betula pendula*, *Fagus sylvatica*, as medium decay (C/N < 60 and decay less then 2-3 years), and the species with C/N > 60 and more then three years decay are considered as having recalcitrant foliage. Data about litter quality could be found in Lyr *et al.* (1992) giving for some species indications about the nitrogen concentration (%) compared to the dry substance. Recalculating the C/N for species like *Sambucus nigra*, *H. rhamnoides*, *Viburnum* spp., *Prunus domestica*, *Prunus avium* indications about litter quality could be obtained. In Wilmanns (1993) the litter of the *Alnus* spp., *Ulmus* spp, *Robinia pseudo-acacia* and *Fraxinus excelsior* is described as fast decomposing and was therefore considered as fast decaying litter. Neither of the remaining deciduous species, as *Amelanchier ovalis*, *Berberis vulgaris*, *Cornus sanguinea*, *Crataegus laevigata*, *Crataegus monogyna*, *Frangula alnus*, *Ilex aquifolium*, *Juglans regia*, *Ligustrum vulgare*, *Lonicera xylosteum, Malus sylvestris*, was cited in the literature as being fast or slowly decomposing. Therefore medium decay is associated to these species. Ehlers (1960) assigned to *Populus tremula* fast decaying foliage litter.

**FTol (***1 = very low tolerance, 5 = very high tolerance*)
For details, see Chapter 3.

**MOR**
The modulus of rupture (MOR; N/mm$^2$) was derived based on Vorreiter (1949), Kollman (1951), Wagenführ and Scheiber (1989), Sell (1989), Lohmann (1991) and Dahms (1996). As no data could be collected for *Salix* species other then *Salix alba*, the value of *Salix alba* was considered to be representative for all *Salix* species. The same is valid for the *Acer* spp. in case of *Acer platanoides* and for *Prunus padus* and *Prunus domestica* in case of *Prunus avium*. For the remaining species, like *Juniperus*

*communis, Alnus incana, Alnus viridis, Amelanchier ovalis, Berberis vulgaris, Cornus sanguinea, Corylus avellana, Crataegus laevigata, Crataegus monogyna, Frangula alnus, Hippophae rhamnoides, Ilex aquifolium, Ligustrum vulgare, Lonicera xylosteum, Malus sylvestris, Prunus mahaleb, Prunus spinosa, Rhamnus cathartica, Viburnum lantana* and *Viburnum opulus* a mean value (=91 N/mm$^2$) has been calculated of the species for which data were available. To note that shrub species may have lower values of MOR then the calculated mean value.

### *mCw / kcw*

Crown diameter varies with the development stage of an individual tree or shrub, its social status within a stand and with the availability of resources. Up to now, numerous crown width models exists (Schmidt, 2001), but following Bragg (2001), the most common form is a simple, non-linear power function where $C_D$ is a function of diameter at breast height (DBH) and species specific regression coefficients. However, linear relationships with DBH were also used in cases where data availability was limited (Nagel *et al.,* 2001). Relation to DBH is given, as maximum crown size is naturally constraint by DBH in view of mechanical tree stability and in view of the assimilation capacity of the crown. Crown diameter measures make not yet part of the large-scale national forest inventory in Switzerland (LFI). Data were recorded in specific studies, as for example in forest health inventories, in which tree health of the main tree species is evaluated by their crown characteristics (*e.g.* 'Swiss National Forest Health Inventory, 'Sanasilva 1997'; Brang, 1998). To obtain empirical relationships between the output of RIFOD and the crown diameter ($C_D$), single-tree data from the 'Sanasilva 1997' were evaluated. However, not for every species sufficient data were available; therefore a distinction has been made between coniferous and deciduous tree species, and within the deciduous species, between species with typically larger or smaller crowns. The available species-specific data were aggregated based on indications of Clouston (1991) and others. Typically wide crown trees are *Aesculus hippocastanum, Carpinus betulus*, *Fagus sylvatica, Fraxinus excelsior*, *Quercus robur* and *Tilia* spp. The other species belong to the group with smaller (more tight) crowns. On the aggregated Sanasilva data a non-linear model have been fitted to the DBH (cm) measures of deciduous species and coniferous species see Equation (1). As data of 'Sanasilva 1997' cover only trees over a diameter greater then 12 cm, a linear interpolation has been made for diameters between 0 and 12 cm. For the shrub species the crown expansion is estimated by a crown dimension factor (= $c_4$), based on the collected data of Geyer (1997). This dimension factor relates height H (m) of a tree or shrub to its crown diameter $C_D$; see Equation (2). The estimated non-linear regression coefficients ($c_1$ to $c_3$) are given in Table 1.

Model 1: $C_D = c_1 + c_2 \cdot DBH^{c_3}$   (for DBH > 12 cm)   (1)

Model 4: $C_D = c_4 \cdot H$               (2)

Table 1: Crown width models for deciduous and coniferous tree
species based on data of 'Sanasilva 1997.

| | df | $c_1$ | Std. error | t value | $c_2$ | Std. error | t value | $c_3$ | Std. error | t value | RSE |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Deciduous spp. with 'smaller' crowns | 354 | 0.679 | 0.688 | 0.986 | 8.100 | 0.356 | 22.759 | 0.761 | 0.178 | 4.262 | 0.815 |
| Deciduous spp. with 'larger' crowns | 726 | 1.745 | 0.296 | 5.895 | 9.300 | 0.321 | 28.977 | 1.096 | 0.120 | 9.161 | 1.170 |
| Coniferous spp. | 2035 | 0.879 | 0.256 | 4.429 | 5.729 | 0.167 | 34.332 | 0.743 | 0.077 | 9.650 | 0.834 |

Compared to measured crown diameters of solitary deciduous trees, the calculated crown diameters seem small. This is mainly due to the fact, that within a forest stand horizontal crown expansion is affected by inter-specific competition for space and resources. To note that there exist also species which following the environmental conditions develop either as a tree or as a shrub (*e.g. Salix eleagnos, Salix fragilis, Salix pentandra, Salix triandra* or *Sambuccus nigra*). In conditions of regular disturbance of shoot development (*e.g.* loss of biomass; Bellingham and Sparrow, 2000) or of limited resources (*e.g.* light, water, nutrients), these species develop preferentially as a shrub. It allows them exploiting more rapidly the available space and growing under limited resources. The coefficient c4 (= $k_{cw}$) for the shrub species is listed in Table 3.

### *mCL*

The determination of the parameter mCL has been described in Chapter 6, page 101 to 102. In addition, the classification performance was compared to the relative majority rule (RMR). As tree classification analysis including coniferous species type as independent variable did not reveal 'species type' as important for classification in crown lengths categories all coniferous species have been grouped – in opposition to the deciduous species. Deciduous species with only few data have been grouped into 'other broadleaf species', the others for sake of simplicity by genus type. In Table 2 the comparison of the tree misclassification error rate versus the relative majority rule can be found. N is the number of individuals in the sample, MER denotes the misclassification error rate, cp the complexity parameter, RMR the error rate using

the relative majority rule and IMP, the improvement of correct classification using classification tree analysis.

Table 2: Comparison of tree misclassification error rate versus the relative majority rule.

| mCL | | N | MER (%) | cp | RMR (%) | IMP (%) |
|---|---|---|---|---|---|---|
| | Broadleaf species | 27434 | 38.06 | 0.0015 | 38.80 | 0.75 |
| 1 | *Acer* spp. | 2513 | 40.31 | 0.0055 | 48.62 | 8.31 |
| 2 | *Alnus* spp. | 1132 | 32.77 | 0.01 | 42.49 | 9.72 |
| 3 | *Betula pendula* | 890 | 31.69 | 0.015 | 40.56 | 8.88 |
| 4 | *Carpinus betulus* | 320 | 14.06 | 0.0155 | 17.50 | 3.44 |
| 5 | *Castanea sativa* | 1416 | 28.51 | 0.0096 | 36.13 | 7.62 |
| 6 | *Fagus sylvatica* | 13124 | 30.07 | 0.0013 | 30.62 | 0.57 |
| 7 | *Fraxinus excelsior* | 2418 | 38.54 | 0.005 | 46.24 | 7.69 |
| 8 | *Populus* spp. | 179 | 21.23 | 0.0013 | 44.13 | 22.91 |
| 9 | *Quercus* spp. | 1549 | 37.96 | 0.008 | 49.32 | 11.36 |
| 10 | *Salix* spp. | 223 | 24.66 | 0.009 | 34.08 | 9.42 |
| 11 | *Tilia* spp. | 500 | 25.60 | 0.025 | 34.20 | 8.60 |
| 12 | *Ulmus* spp. | 237 | 28.69 | 0.035 | 43.46 | 14.77 |
| 13 | Other broadleaf spp. | 564 | 35.64 | 0.014 | 49.29 | 13.65 |
| 14 | Coniferous species | 44712 | 28.17 | 0.03 | 32.55 | 4.38 |

The classifications revealed that the diameter at breast height and height are not of prior importance in determining crown length. Although the variables considered in the classification vary from one genus to another, the variables expressing competition, as well as the ones expressing site characteristics, reduce deviance in the classification process.

***Rotype*** *(1 = shallow rooting type, 3 = deep rooting type)*
For details, see Chapter 5.

***Seedinput / BDisp / EDisp / seedMaxage / SeedGerm / SeedLoss***
For details, see Chapter 6, page 114 to117.

***TCW***
Data of the thousand corn weight (TCW) were obtained from the Swiss Federal Institute of Forest, Snow and Landscape Research (WSL) (http://www.wsl.ch/lm/garten/samen_302-de.ehtml).
For the species *Prunus mahaleb* and *Quercus pubescens* no data could be collected. Hence, the average value of *Quercus robur* and *Quercus petreae* has been assigned to *Quercus pubescens*. *Prunus mahaleb* was set equal to *Prunus avium*.

### rotspr, trkspr, tfspr

Based on Ehlers (1960), Koop (1987), Schiechtl (1992), Lange and Lecher (1993), Kräuchi (1994) and Karrenberg (2003), we distinguished between root suckers, trunk sprouts and sprouts of transported fragments. Following Karrenberg (2002) *Salix* spp. do not develop any root suckers in opposition to *Populus* spp.

### kbrows

This parameter was derived based on indications of Ehlers (1960) and Burschel and Huss (1997).

## Table 3: Estimated parameter values of Central European tree and shrub species for the model RIFOD.

| Species | Abbrv | sType/B | sType/H | sType/N | Dmax | Hmax | Amax | Gr | DrTol | NTol | lighs | ligha | Lq | FTol | Mor | mCW | mCL | Rotype | Sedinp | BDisp | EDisp | TCW | rotspr | trkspr | tfspr | kbrow | kcw | Seed Germ | Seed Loss | Seed MaxAge |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | - | - | - | - | cm | m | yrs | cm/yr | - | - | - | - | - | - | N/mm² | - | - | - | - | - | - | g | - | - | - | - | - | - | - | yrs |
| Abies alba | Aa | C | T | 5 | 215 | 60 | 700 | 209 | 3 | 2 | 3 | 1 | 2 | 1 | 69 | 1 | 14 | 2 | 0.024 | 274 | 304 | 43.6 | 0 | 0 | 0 | 3 | -999.9 | 0.46 | 0.8 | 1 |
| Juniperus communis | Jc | C | S | 5 | 50 | 4 | 1450 | 94 | 5 | 1 | 9 | 9 | 3 | 1 | 91 | 4 | 0 | 2 | 0.101 | 305 | 334 | 4.2 | 0 | 0 | 0 | 2 | 0.5 | 0.5 | 0.8 | 2 |
| Larix decidua | Ld | D | T | 2 | 185 | 52 | 850 | 135 | 2 | 1 | 8 | 9 | 3 | 1 | 96 | 1 | 14 | 3 | 0.068 | 74 | 181 | 7.9 | 0 | 0 | 0 | 2 | -999 | 0.39 | 0.8 | 6 |
| Picea abies | Pa | C | T | 5 | 210 | 58 | 930 | 255 | 1 | 2 | 5 | 5 | 3 | 1 | 71 | 1 | 14 | 1 | 0.070 | 45 | 105 | 7.6 | 0 | 0 | 0 | 2 | -999 | 0.76 | 0.8 | 6.6 |
| Pinus silvestris | Ps | C | T | 4 | 155 | 45 | 760 | 181 | 5 | 1 | 7 | 9 | 3 | 2 | 88 | 1 | 14 | 3 | 0.091 | 60 | 120 | 4.9 | 0 | 0 | 0 | 2 | -999 | 0.91 | 0.8 | 7 |
| Taxus baccata | Tb | C | T | 5 | 355 | 22 | 2110 | 92 | 4 | 2 | 4 | 3 | 2 | 2 | 85 | 1 | 14 | 2 | 0.021 | 305 | 334 | 50 | 0 | 0 | 0 | 3 | -999 | 0.6 | 0.8 | 4.5 |
| Acer campestre | Ac | D | T | 2 | 80 | 23 | 170 | 152 | 4 | 3 | 5 | 5 | 2 | 3 | 101 | 3 | 1 | 2 | 0.015 | 274 | 365 | 91.4 | 0 | 1 | 0 | 1 | -999 | 0.8 | 0.8 | 2.8 |
| Acer platanoides | Ap | D | T | 3 | 170 | 32 | 380 | 175 | 3 | 2 | 2 | 4 | 2 | 2 | 101 | 3 | 1 | 3 | 0.012 | 274 | 365 | 128.7 | 0 | 1 | 0 | 1 | -999 | 0.55 | 0.8 | 2.8 |
| Acer pseudoplatanus | As | D | T | 3 | 215 | 37 | 550 | 111 | 3 | 2 | 2 | 4 | 2 | 1 | 101 | 3 | 1 | 3 | 0.013 | 274 | 365 | 111 | 0 | 1 | 0 | 1 | -999 | 0.6 | 0.8 | 2.1 |
| Aesculus hippocastanum | Ah | D | T | 3 | 140 | 31 | 260 | 279 | 2 | 2 | 4 | 4 | 2 | 2 | 64 | 2 | 13 | 2 | 0.001 | 305 | 334 | 9000 | 0 | 0 | 0 | 2 | -999 | 0.5 | 0.8 | 2 |
| Alnus glutinosa | Ag | D | T | 2 | 130 | 31 | 240 | 263 | 1 | 3 | 5 | 5 | 1 | 5 | 91 | 3 | 2 | 3 | 0.207 | 305 | 90 | 1.3 | 1 | 1 | 0 | 2 | -999 | 0.4 | 0.8 | 4 |
| Alnus incana | Ai | D | T | 2 | 160 | 22 | 150 | 491 | 1 | 2 | 6 | 7 | 1 | 4 | 91 | 3 | 2 | 3 | 0.270 | 121 | 181 | 0.8 | 1 | 1 | 0 | 2 | -999 | 0.33 | 0.8 | 5.5 |
| Alnus viridis | Av | D | S | 2 | 20 | 4 | 100 | 160 | 2 | 2 | 7 | 7 | 1 | 4 | 91 | 4 | 0 | 1 | 0.380 | 121 | 181 | 0.5 | 1 | 1 | 0 | 2 | 0.5 | 0.15 | 0.8 | 5 |
| Amelanchier ovalis | Ao | D | S | 1 | 45 | 3 | 50 | 254 | 5 | 1 | 7 | 7 | 2 | 1 | 91 | 4 | 0 | 3 | 0.020 | 152 | 181 | 56.6 | 0 | 0 | 0 | 2 | 1 | 0.5 | 0.8 | 2 |
| Berberis vulgaris | Bv | D | S | 1 | 20 | 4 | 80 | 86 | 5 | 1 | 7 | 7 | 2 | 2 | 91 | 4 | 0 | 3 | 0.067 | 243 | 334 | 8.2 | 0 | 1 | 0 | 2 | 1 | 0.5 | 0.8 | 2 |
| Betula pendula | Bp | D | T | 1 | 115 | 29 | 220 | 310 | 2 | 1 | 7 | 9 | 2 | 2 | 134 | 3 | 3 | 1 | 0.433 | 213 | 283 | 0.4 | 0 | 1 | 0 | 1 | -999 | 0.19 | 0.8 | 2 |
| Carpinus betulus | Cb | D | T | 3 | 110 | 27 | 220 | 92 | 3 | 2 | 4 | 3 | 1 | 2 | 137 | 2 | 4 | 3 | 0.024 | 274 | 334 | 45.6 | 0 | 1 | 0 | 3 | -999 | 0.67 | 0.8 | 6.3 |
| Castanea sativa | Cs | D | T | 3 | 355 | 33 | 1510 | 66 | 4 | 1 | 5 | 5 | 2 | 2 | 73 | 3 | 5 | 3 | 0.001 | 305 | 334 | 7150 | 0 | 1 | 0 | 2 | -999 | 0.58 | 0.8 | 0.5 |
| Cornus sanguinea | Cn | D | S | 2 | 20 | 5 | 60 | 177 | 3 | 2 | 7 | 7 | 2 | 3 | 91 | 4 | 0 | 1 | 0.020 | 243 | 334 | 56.6 | 0 | 1 | 0 | 2 | 0.5 | 0.5 | 0.8 | 2 |
| Corylus avellana | Ca | D | S | 3 | 70 | 10 | 70 | 202 | 4 | 2 | 6 | 6 | 1 | 2 | 91 | 4 | 0 | 2 | 0.003 | 244 | 334 | 1135 | 0 | 1 | 0 | 3 | 0.5 | 0.5 | 0.8 | 1.5 |
| Crataegus laevigata | Cl | D | S | 1 | 20 | 9 | 400 | 74 | 5 | 3 | 6 | 6 | 2 | 1 | 91 | 4 | 0 | 3 | 0.021 | 243 | 334 | 53.4 | 0 | 1 | 0 | 2 | 1 | 0.5 | 0.8 | 2 |
| Crataegus monogyna | Cm | D | S | 1 | 30 | 12 | 450 | 90 | 5 | 1 | 7 | 7 | 2 | 2 | 91 | 4 | 0 | 3 | 0.015 | 243 | 334 | 90 | 0 | 1 | 0 | 2 | 1 | 0.5 | 0.8 | 2 |
| Fagus silvatica | Fs | D | T | 3 | 225 | 45 | 430 | 175 | 2 | 1 | 3 | 1 | 2 | 1 | 116 | 2 | 6 | 2 | 0.009 | 289 | 314 | 217.5 | 1 | 1 | 0 | 3 | -999 | 0.71 | 0.8 | 3.3 |
| Frangula alnus | Fa | D | S | 2 | 20 | 6 | 60 | 574 | 3 | 1 | 7 | 7 | 2 | 4 | 91 | 4 | 0 | 1 | 0.041 | 213 | 304 | 18.2 | 1 | 1 | 0 | 2 | 1.5 | 0.5 | 0.8 | 2 |
| Fraxinus excelsior | Fe | D | T | 2 | 190 | 42 | 350 | 222 | 2 | 3 | 4 | 6 | 1 | 3 | 112 | 2 | 7 | 2 | 0.021 | 32 | 90 | 52.9 | 0 | 1 | 0 | 2 | -999 | 0.6 | 0.8 | 3.7 |
| Hippophae rhamnoides | Hr | D | S | 1 | 20 | 7 | 60 | 211 | 5 | 1 | 9 | 9 | 1 | 3 | 91 | 4 | 0 | 3 | 0.056 | 243 | 334 | 11 | 1 | 0 | 0 | 2 | 0.5 | 0.5 | 0.8 | 2 |
| Ilex aquifolium | Ia | D | S | 3 | 60 | 17 | 330 | 76 | 2 | 2 | 4 | 4 | 2 | 1 | 91 | 4 | 0 | 1 | 0.028 | 305 | 31 | 34.4 | 1 | 0 | 0 | 2 | 0.5 | 0.5 | 0.8 | 2 |
| Juglans regia | Jr | D | T | 3 | 140 | 29 | 470 | 167 | 3 | 3 | 6 | 6 | 2 | 2 | 133 | 3 | 13 | 3 | 0.001 | 273 | 334 | 10000 | 0 | 0 | 0 | 2 | -999 | 0.5 | 0.8 | 2 |
| Ligustrum vulgare | Lv | D | S | 3 | 20 | 5 | 50 | 209 | 4 | 1 | 7 | 7 | 2 | 3 | 91 | 4 | 0 | 1 | 0.041 | 213 | 30 | 18.4 | 0 | 0 | 0 | 2 | 1 | 0.5 | 0.8 | 2 |
| Lonicera xylosteum | Lx | D | S | 1 | 20 | 3 | 50 | 409 | 4 | 2 | 5 | 5 | 2 | 3 | 91 | 4 | 0 | 3 | 0.104 | 182 | 273 | 4 | 0 | 0 | 0 | 2 | 1 | 0.5 | 0.8 | 2 |
| Malus sylvestris | Ms | D | T | 3 | 45 | 11 | 170 | 106 | 3 | 3 | 7 | 7 | 1 | 2 | 91 | 3 | 13 | 1 | 0.029 | 243 | 334 | 32.1 | 0 | 0 | 0 | 2 | -999 | 0.5 | 0.8 | 2 |
| Populus alba | Pa | D | T | 2 | 175 | 33 | 440 | 208 | 2 | 3 | 5 | 5 | 2 | 3 | 60 | 3 | 8 | 3 | 0.653 | 121 | 181 | 0.2 | 1 | 1 | 1 | 2 | -999 | 0.5 | 0.8 | 2 |
| Populus nigra | Pn | D | T | 2 | 190 | 36 | 280 | 249 | 1 | 2 | 5 | 5 | 2 | 4 | 60 | 3 | 8 | 3 | 0.653 | 121 | 181 | 0.2 | 1 | 1 | 1 | 3 | -999 | 0.2 | 0.8 | 0.6 |
| Populus tremula | Pt | D | T | 2 | 125 | 30 | 140 | 293 | 3 | 2 | 6 | 7 | 2 | 3 | 37 | 3 | 8 | 3 | 0.653 | 121 | 181 | 0.2 | 1 | 1 | 1 | 3 | -999 | 0.2 | 0.8 | 2 |
| Prunus avium | Pa | D | T | 3 | 50 | 30 | 240 | 137 | 3 | 2 | 4 | 4 | 1 | 1 | 84 | 3 | 13 | 1 | 0.010 | 213 | 243 | 185 | 1 | 1 | 0 | 2 | -999 | 0.5 | 0.8 | 2 |
| Prunus domestica | Pd | D | T | 3 | 30 | 12 | 80 | 223 | 2 | 2 | 5 | 5 | 1 | 4 | 80 | 3 | 13 | 2 | 0.007 | 305 | 334 | 331 | 0 | 0 | 0 | 2 | -999 | 0.5 | 0.8 | 2 |
| Prunus mahaleb | Pm | D | S | 2 | 20 | 11 | 60 | 255 | 5 | 1 | 7 | 7 | 1 | 1 | 91 | 4 | 0 | 3 | 0.010 | 213 | 304 | 185 | 0 | 1 | 0 | 2 | 1 | 0.5 | 0.8 | 2 |
| Prunus padus | Pp | D | T | 2 | 60 | 15 | 70 | 308 | 2 | 2 | 5 | 5 | 1 | 4 | 84 | 3 | 13 | 2 | 0.025 | 244 | 334 | 40.1 | 1 | 1 | 0 | 2 | -999 | 0.5 | 0.8 | 2 |
| Prunus spinosa | Ps | D | S | 2 | 20 | 5 | 60 | 255 | 4 | 2 | 7 | 7 | 1 | 2 | 91 | 4 | 0 | 2 | 0.010 | 305 | 59 | 184.1 | 0 | 0 | 0 | 2 | 1.5 | 0.5 | 0.8 | 2 |
| Quercus petraea | Qp | D | T | 3 | 285 | 45 | 860 | 91 | 3 | 1 | 6 | 7 | 2 | 1 | 102 | 3 | 9 | 3 | 0.002 | 274 | 304 | 2850 | 0 | 1 | 0 | 2 | -999 | 0.69 | 0.8 | 2.6 |
| Quercus pubescens | Qu | D | T | 3 | 90 | 25 | 500 | 202 | 4 | 2 | 7 | 7 | 2 | 1 | 95 | 3 | 9 | 3 | 0.002 | 274 | 304 | 3711 | 0 | 1 | 0 | 2 | 0.5 | 0.7 | 0.8 | 1 |
| Quercus robur | Qr | D | T | 3 | 320 | 52 | 1060 | 199 | 5 | 1 | 7 | 9 | 2 | 3 | 92 | 2 | 9 | 3 | 0.001 | 274 | 304 | 4572 | 0 | 1 | 0 | 2 | -999 | 0.75 | 0.8 | 1.8 |
| Rhamnus cathartica | Rc | D | S | 1 | 20 | 7 | 90 | 160 | 5 | 1 | 7 | 7 | 1 | 3 | 91 | 4 | 0 | 3 | 0.043 | 243 | 334 | 16.5 | 1 | 0 | 0 | 2 | 1 | 0.5 | 0.8 | 2 |
| Robinia pseudoacacia | Rp | D | T | 2 | 120 | 28 | 310 | 294 | 5 | 3 | 5 | 5 | 1 | 2 | 134 | 3 | 13 | 3 | 0.060 | 32 | 90 | 9.9 | 1 | 1 | 0 | 2 | -999 | 0.5 | 0.8 | 2 |
| Salix alba | Sa | D | T | 1 | 100 | 27 | 170 | 318 | 1 | 3 | 5 | 5 | 2 | 5 | 43 | 3 | 10 | 3 | 1 | 121 | 181 | 0.1 | 0 | 1 | 1 | 1 | -999 | 0.2 | 0.8 | 1 |
| Salix appendiculata | Sn | D | S | 1 | 20 | 6 | 60 | 433 | 1 | 2 | 5 | 7 | 2 | 4 | 43 | 4 | 0 | 3 | 1 | 121 | 181 | 0.1 | 0 | 1 | 1 | 2 | 0.75 | 0.2 | 0.8 | 1 |
| Salix caprea | Sc | D | T | 1 | 60 | 15 | 80 | 358 | 3 | 3 | 5 | 7 | 2 | 4 | 43 | 3 | 0 | 3 | 1 | 121 | 181 | 0.1 | 0 | 1 | 1 | 2 | 0.5 | 0.2 | 0.8 | 1 |
| Salix cinerea | Si | D | S | 1 | 20 | 8 | 65 | 274 | 1 | 1 | 5 | 7 | 2 | 5 | 43 | 4 | 0 | 3 | 1 | 121 | 181 | 0.1 | 0 | 1 | 1 | 2 | 1.5 | 0.2 | 0.8 | 1 |
| Salix daphnoides | Sd | D | T | 1 | 80 | 17 | 40 | 475 | 3 | 1 | 5 | 6 | 2 | 5 | 43 | 3 | 10 | 3 | 1 | 121 | 181 | 0.1 | 0 | 1 | 1 | 2 | 0.5 | 0.2 | 0.8 | 1 |
| Salix elaeagnos | Se | D | T | 1 | 80 | 12 | 50 | 433 | 3 | 1 | 5 | 7 | 2 | 5 | 43 | 3 | 10 | 3 | 1 | 121 | 181 | 0.1 | 0 | 1 | 1 | 2 | 0.5 | 0.2 | 0.8 | 1 |
| Salix fragilis | Sf | D | T | 1 | 80 | 11 | 60 | 347 | 1 | 2 | 5 | 5 | 2 | 5 | 43 | 3 | 10 | 3 | 1 | 121 | 181 | 0.1 | 0 | 1 | 1 | 2 | 0.5 | 0.2 | 0.8 | 1 |
| Salix myrsi. nigricans | Sm | D | S | 1 | 20 | 4 | 50 | 433 | 1 | 2 | 5 | 7 | 2 | 5 | 43 | 4 | 0 | 3 | 1 | 121 | 181 | 0.1 | 0 | 1 | 1 | 2 | 1 | 0.2 | 0.8 | 1 |
| Salix pentandra | Sp | D | T | 1 | 80 | 12 | 60 | 433 | 1 | 1 | 5 | 7 | 2 | 5 | 43 | 3 | 10 | 3 | 1 | 121 | 181 | 0.1 | 0 | 1 | 1 | 2 | 0.5 | 0.2 | 0.8 | 1 |
| Salix purpurea | Su | D | S | 1 | 40 | 8 | 50 | 463 | 3 | 1 | 5 | 8 | 2 | 4 | 43 | 4 | 0 | 3 | 1 | 121 | 181 | 0.1 | 0 | 1 | 1 | 2 | 0.5 | 0.2 | 0.8 | 1 |
| Salix triandra | St | D | S | 1 | 50 | 9 | 60 | 433 | 1 | 2 | 5 | 7 | 2 | 4 | 43 | 4 | 0 | 3 | 1 | 121 | 181 | 0.1 | 0 | 1 | 1 | 2 | 0.75 | 0.2 | 0.8 | 1 |
| Salix viminalis | Sv | D | S | 1 | 50 | 10 | 60 | 600 | 1 | 2 | 5 | 7 | 2 | 5 | 43 | 4 | 0 | 3 | 1 | 121 | 181 | 0.1 | 0 | 1 | 1 | 2 | 1.5 | 0.2 | 0.8 | 1 |
| Sambucus nigra | Sb | D | S | 2 | 30 | 6 | 130 | 397 | 4 | 3 | 5 | 7 | 1 | 2 | 91 | 4 | 13 | 1 | 0.118 | 213 | 304 | 3.3 | 0 | 1 | 0 | 2 | 0.5 | 0.2 | 0.8 | 1 |
| Sorbus aria | So | D | T | 1 | 55 | 22 | 860 | 173 | 4 | 2 | 6 | 7 | 1 | 2 | 101 | 3 | 0 | 3 | 0.042 | 305 | 334 | 17.1 | 0 | 1 | 0 | 2 | 0.5 | 0.2 | 0.8 | 4.3 |
| Sorbus aucuparia | Sr | D | T | 1 | 65 | 19 | 110 | 217 | 4 | 1 | 6 | 7 | 1 | 3 | 105 | 3 | 0 | 3 | 0.108 | 305 | 334 | 3.7 | 1 | 1 | 0 | 2 | 0.5 | 0.7 | 0.8 | 8 |
| Tilia cordata | Tc | D | T | 3 | 230 | 30 | 940 | 119 | 4 | 2 | 5 | 5 | 2 | 2 | 100 | 2 | 11 | 2 | 0.025 | 289 | 365 | 39.4 | 0 | 1 | 0 | 2 | -999 | 0.45 | 0.8 | 2.9 |
| Tilia platyphyllos | Tp | D | T | 3 | 405 | 39 | 960 | 140 | 3 | 3 | 4 | 3 | 2 | 1 | 99 | 2 | 11 | 2 | 0.015 | 289 | 365 | 97.1 | 0 | 1 | 0 | 2 | -999 | 0.48 | 0.8 | 2.5 |
| Ulmus scabra | Us | D | T | 3 | 195 | 43 | 480 | 210 | 3 | 3 | 4 | 3 | 1 | 1 | 78 | 3 | 12 | 2 | 0.048 | 152 | 197 | 13.9 | 1 | 1 | 0 | 1 | -999 | 0.35 | 0.8 | 7.7 |
| Ulmus minor | Um | D | T | 3 | 200 | 40 | 470 | 196 | 4 | 3 | 5 | 5 | 1 | 3 | 80 | 3 | 12 | 3 | 0.058 | 152 | 197 | 10.3 | 1 | 1 | 0 | 2 | -999 | 0.5 | 0.8 | 7.7 |
| Viburnum lantana | Vl | D | S | 2 | 20 | 6 | 90 | 300 | 5 | 2 | 6 | 6 | 2 | 2 | 91 | 4 | 0 | 3 | 0.024 | 244 | 334 | 43.7 | 0 | 1 | 0 | 2 | 1 | 0.5 | 0.8 | 2 |
| Viburnum opulus | Vo | D | S | 2 | 20 | 5 | 40 | 300 | 2 | 2 | 8 | 8 | 2 | 3 | 91 | 4 | 0 | 1 | 0.031 | 213 | 304 | 29.1 | 0 | 1 | 0 | 2 | 0.5 | 0.5 | 0.8 | 2 |

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# ACKNOWLEDGEMENTS

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Born on the 1st of April, 1973 in Sierre (Valais)
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### Education

| | |
|---|---|
| April 2005 | PhD in environmental science at the Laboratory of Ecosystem Management, École Polytechnique Fédérale de Lausanne (EPFL). PhD thesis: 'Process-based, spatially-explicit modelling of riparian forest dynamics in Central Europe - Tool for decision-making in river restoration'. Supervisor: Prof. Rodolphe Schlaepfer (EPFL), Referees: Dr. F. Kienast (WSL), Prof. P. Edwards (ETHZ), Dr. H. Lischke (WSL), Dr. I. Iorgulescu (EPFL). |
| 2001-2005 | PhD student in environmental science at the Laboratory of Ecosystem Management, EPFL. |
| March 1999 | Postgraduate diploma in environmental science at the Laboratory of Ecosystem Management, EPFL. Thesis: ‚Lebensraumanalyse des Wolf für das Wallis mit Hilfe von GIS'. Supervisor: Prof. Rodolphe Schlaepfer. |
| 1997-1999 | Postgraduate course in environmental science at the EPFL. |
| 1993 – 1997 | Majored in biology (zoology, human physiology, botanic) at the University of Lausanne (UNIL). |
| July 1992 | Degree in socio-economics ('Eidgenössische Maturität Typus E'). College 'Spiritus Sanctus', Brig. |

### Work Experience

| | |
|---|---|
| Feb. 2000 - Aug. 2001 | Project manager of WWF Oberwallis (60%). |
| June 1999 - Aug. 2001 | Scientific collaborator at the Laboratory of Ecosystem Management. Coordinator of a project between WWF International, IUCN and the EPFL, entitled 'Development of criteria and indicators of forest quality at landscape scale'. |

### Research Experience

| | |
|---|---|
| Nov. 1999 – Feb. 2000 | Simulation of wolf (*Canis lupus*) spreading movements from different arrival points in the southern part of Switzerland (Canton of Valais), Joint work with Dr Diego Kuonen, Department of Mathematics, EPFL. |
| March 1997 - June 1997 | Determination of forest dynamics in the Jura mountains (from 1940-1990) by using photo interpretation methods, certificate report, University of Lausanne. |
| Oct. 1996 - Jan. 1997 | Effects of the vitamins E and C on the embryonic chicken heart (in anoxic and oxic conditions), certificate report, University of Lausanne. |

**Publications**

Glenz C, Schlaepfer R, Iorgulescu I, Kienast F. 2005 (submitted). Flooding tolerance of trees and shrubs - Case of Central European species. *Forest Ecology and Management*.

Glenz C, Iorgulescu I, Kienast F, Schlaepfer R. 2005 (submitted). Modelling flooding tolerance of tree species using fuzzy logic. *Ecological Modelling*.

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Glenz C, Massolo A, Kuonen D, Schlaepfer R. A wolf habitat suitability prediction study in Valais (Switzerland). 2001. *Landscape and Urban Planning*, 55, 55-65.

**Workshops and Congresses**

July 13. - 17. 2003
'Adapting Gap models to fluvial landscapes by accounting for geomorphological and hydraulic processes'. Glenz C, Iorgulescu I, Schlaepfer R, Kienast F. 6th International Association for Landscape Ecology World Congress, Darwin (oral presentation).

April 6. - 11. 2003
'Modelling the dynamics of riparian forests by accounting for hydraulic and geomorphological processes'. Glenz C, Iorgulescu I, Kienast F, Schlaepfer R. EGS-AGU-EUG Joint Assembly Nice, France (poster).

Nov. 15. - 16. 2001
'Impact of flooding on growth, physiology and disease susceptibility of trees in floodplain forests and artificially flooded forest stands'. International Workshop. Freiburg (D) (oral presentation).

Oct. 23. - 25. 2000
IUCN/WWF Workshop, Vissoie (Switzerland), 'Using a landscape approach to forest conservation'.

May 29. - June 3. 1999
'Predicting wolf (*Canis lupus*) presence and reproduction sites and simulation of spreading movements from different arrival points'. Glenz C, Massolo A, Kuonen D, Schlaepfer R. 3rd European Congress of Mammology, Jvskyla, Finland (Poster).

**Languages**

German; mother tongue
French; spoken, read, written
Italian; spoken, read, fairly written
English; spoken, read, written

**Special Skills**

Founder and vice-president of the organization 'D'Obru Alumni'
Former president of the communal environmental commission, Salgesch
Former comity member of D'Obru, Lausanne
Comity member of WWF Oberwallis