Doctoral Thesis

Inter- and intraspecific competition in mixed Pinus sylvestris and Quercus pubescens stands - Modelling stand dynamics based on tree-ring analysis

Author(s):
Weber, Pascale

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Inter- and intraspecific competition in mixed *Pinus sylvestris* and *Quercus pubescens* stands – Modelling stand dynamics based on tree-ring analysis

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SWISS FEDERAL INSTITUTE OF TECHNOLOGY
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presented by

Pascale Anja Weber

Dipl. Umwelt-Natw. ETH
Born 12th August, 1972
Citizen of Zürich

accepted on the recommendation of

Prof. Dr. Harald Bugmann, examiner
Dr. Andreas Rigling, co-examiner
PD Dr. Felix Kienast, co-examiner

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Summary

In Valais, one of the driest valleys of the Alps, the large-scale low-elevation pine forests are shifting towards mixed deciduous forests. The evergreen sub-boreal Scots pine (*Pinus sylvestris* L.) shows high mortality rates, whereas the deciduous sub-Mediterranean pubescent oak (*Quercus pubescens* Willd.) is becoming more abundant. Many factors are thought to play a mutual role in these processes. The thesis presented here examines changes in the competitive ability of both species as a consequence of natural succession, changed forest-use practices and increasing drought due to climatic changes, and aims at providing a scientific basis for forest management and conservation. The specific objectives were 1) to identify autecological differences between Scots pine and pubescent oak, 2) to retrospectively trace intra- and interspecific competition in mixed Scots pine and pubescent oak stands and 3) to evaluate the impact of forest grazing on past stand dynamics and current species composition of the xeric low-elevation forests in Valais.

In chapters I and IV, autecological differences in the adaptation to drought between Scots pine and pubescent oak were studied using dendroecological and wood anatomical methods. At the tree-ring level, response function analysis was utilised to analyse the species-specific growth response to moisture availability on fifteen sampling plots situated at elevations between 590 and 1200 m a.s.l. While oaks were found to respond mainly to the moisture conditions of the previous autumn and current spring, with a breakdown of the response in July, pines did not start responding before May, but showed responses throughout the whole summer. Moreover, their growth was more strongly related to prior growth, which can be explained by the perennial photosynthetic tissue. In addition, principal component analysis revealed spatial patterns of drought response in both species, which were associated with the sub-regional climate and soil conditions. In contrast to our expectations, the altitudinal gradient did not appear to play a major role in the response patterns. Together with the wood anatomical results on the influence of drought years on the production and formation of water-conduction cells, these results suggest that the growth patterns of both species are strongly determined by the xeric site conditions. However, some of the results in chapter I indicate that pubescent oak is better adapted than Scots pine, if the climate should change further towards more Mediterranean conditions.

In chapter II, a tree-ring based competition index was introduced to reconstruct the competitive dynamics of individual trees over time. This index combines a temporal and spatial component by calculating the yearly ratio between the basal area increments of the neighbouring
trees and the basal area increment of the tree being subjected to the analysis. Such individual
dynamic competition curves for 456 trees from five stands were calculated 40 years back in
time. The curves were clustered into a large group of pines and oaks with constant competi-
tion, and a smaller group of pines with recently increasing competition. In addition, stand
structure analyses indicated a change towards a higher proportion of oak. The changes in
competitive ability between pubescent oak and Scots pine were found to be related to drought
as well as to natural development towards a later successional stage that favours the more
shade-tolerant oak.

Based on the results of the first two parts, the forest gap model ForClim was adapted, and
stand dynamics of the low-elevation forests in Valais were evaluated on a larger temporal
scale (chapter III). In particular, several changes were made in the parameterisation of the
drought-tolerance, shade-tolerance and browsing susceptibility of Scots pine and pubescent
oak in the model. These changes were examined in more detail by a systematic sensitivity
analysis. Using the adapted model version, simulated tree density and basal area was com-
pared with empirical data from eight forest plots. Whereas the model represented pubescent
oak relatively well, Scots pine was underestimated. A more realistic representation of Scots
pine in the model was attained by introducing a forest-history based grazing scenario. The
model application thus suggests that grazing allows for a longer period of codominance of
Scots pine and pubescent oak, and that human impacts had a strong effect on these forests by
delaying the succession in favour of Scots pine.

In conclusion, a rather broad and at the same time detailed understanding of competition and
forest succession in the low-elevation forests of Valais has been obtained by investigating tree
growth from the cell to the stand level and by addressing different questions at different scales
in time and space. It has been shown that pubescent oak and Scots pine are fundamentally
different in their adaptation to drought. Moreover, these differences in the response to mois-
ture availability also seemed to account for some differences in the competitive ability over
time. In the pioneer species Scots pine, the decrease in the competitive ability of a small
group of trees, together with the high proportion of dead branches recorded, indicated a recent
increase in competition for light. Further changes in species composition towards a higher
proportion of oak can thus be expected due to natural succession, but also because the climate
is changing towards more Mediterranean conditions.
Zusammenfassung


Insgesamt konnte mit diesen Analysen von der Zell- bis zur Bestandesebene ein breites und zugleich recht detailliertes Verständnis der Konkurrenz- und Bestandesentwicklung gewonnen werden. Waldöhre und Flaumeiche unterscheiden sich nicht nur grundsätzlich in ihrer Wachstumsreaktion auf klimatische Bedingungen, sondern dies kann sich auch auf die Konkurrenzverhältnisse zwischen den beiden Arten auswirken. Weitere Verschiebungen zugunsten eines höheren Flaumeichenanteils können deshalb nicht nur aufgrund der natürlichen Sukzession, sondern auch in einem wahrscheinlich immer mediterraneren Klima erwartet werden.
General introduction

Scots pine and pubescent oak forests in Valais

For many years, plant sociologists regarded Scots pine (*Pinus sylvestris* L.) forest associations as being the main native forest type at xeric, low-elevation sites in Valais (Braun-Blanquet 1917, Christ 1920, Schmid 1936, Ozenda 1985, Plumettaz Clot 1988). Although some of their works have described oak forest associations in Valais (e.g. Braun-Blanquet 1961, e.g. Schmid 1961b), they usually ascribed them relatively low importance, and they suggested that vineyards have replaced most of the native oak forest area (Braun-Blanquet 1961, Schmid 1961a). For the first time, Burnand (1976) concentrated on investigating the ecological limits of pubescent oak (*Quercus pubescens* Willd.) in Valais. At that time, he had already posed questions on both the natural distribution range of pubescent oak according to its ecological amplitude and the impact of forest management on the occurrence of pubescent oak and Scots pine in Valais.

The distribution area of Scots pine covers the whole Euro-Siberian range, whereas pubescent oak is a typical sub-Mediterranean broad-leaved tree species with a much smaller distributional range (Meusel et al. 1965). However, their distribution areals overlap in mountainous areas in the southern part of Europe, and in some parts of Eastern Europe (Burnand 1976), i.e. in regions that are characterised by sub-continental, sub-Mediterranean climates (Brzeziecki et al. 1995). Studying tree species at the border of their distribution where different species occur in the same ecological niche, such as Scots pine and pubescent oak in Valais (Burnand 1976), can be quite rewarding for better understanding their ecological climate response (Stein 1978).

In Valais, the expansion of pubescent oak into the area occupied by Scots pine forests has only become apparent on a larger spatial scale in recent years. At the beginning of the 20th century, pubescent oak had not appeared frequently in vegetational studies of Valais. Christ (1920) for example reports that, unlike today, there was “hardly any trace” of pubescent oak in the forests around Visp. In contrast, recent vegetation and stand structure data from Valais indicate i) abundant pubescent oak regeneration below 1000 m a.s.l. (Mayer et al. submitted) and ii) a shift in species composition from Scots pine towards deciduous tree species in general, and pubescent oak in particular (WSL 2001, Hadorn 2002, Tinner 2004).
So far, it has remained unclear to what degree pubescent oak will displace Scots pine in the future. Land-use and climate changes complicate the prediction of forest development, in particular at low-elevations where site conditions are rather extreme as documented by frequent summer drought periods (Kuhn 1973). However, the estimation of future forest dynamics is crucial for forest management and conservation. Therefore, this thesis is concerned with changes in the competitive behaviour of Scots pine and pubescent oak as in consequence of natural succession, changed forest-use practices and increasing drought due to climatic changes.

**Current hypotheses for Scots pine decline in Valais**

Not only do the forests of Valais form a characteristic landscape harbouring one of the Swiss biodiversity hotspots (Wohlgemuth 1998), but they often also protect human infrastructure from natural hazards such as avalanches and falling rocks (Pfister & Eggenberger 1988). Because high mortality rates of Scots pine may put these forest functions at risk, their fate is of high socio-economic interest. Thus, scientifically based planning rules are crucial to maintain forest functions.

In Valais, the potential factors for the high Scots pine mortality have therefore repeatedly been studied since the beginning of the 20th century (e.g. Wille 1922). In the 1970s, when extensive research on the Scots pine decline phenomenon was started, damages were reported to cover approximately 130 square kilometres (Flühler et al. 1981). The damage symptoms were described as being randomly distributed on single trees, i.e. vital trees growing in close neighbourhood to damaged trees, which is a pattern not typically found for disturbance agents such as insect attacks. Subsequently, a complex of influencing factors was thought to be responsible for pine decline. Thereby, fluoric air pollution emitted by the aluminium industry was hypothesised as being one cause of the high mortality rates of pine in the short- and in the long-term, besides natural stress factors, forest management and ageing (Flühler et al. 1981, Kienast et al. 1981, Kontic et al. 1986). Already in these earlier studies, pine decline was also surmised to be associated with drought years (Kienast et al. 1981, Kienast 1982).

In 2001, intense research on pine decline was resumed due to alarming mortality rates of pine (approx. 5% per year, i.e. about ten times higher than the Swiss average), although today, pollution as the a main influencing factor can practically be ruled out due to the installation of
filters in the aluminium industry (Rigling & Cherubini 1999). In the ongoing interdisciplinary project “Die Waldföhrenwälder im Wallis - Ein Landschaftselement im Umbruch” (brief “Pine project”), the following hypotheses were formulated for pine decline (Rigling 2002):

1) Scots pine decline is caused by climatic factors in relation to a warming climate (endogenous disturbance):
   a. directly by increasing drought
   b. indirectly by an increasing abundance of insects, phytopathogens and mistletoes with increasing temperature

2) Scots pine decline is caused by non-climatic factors:
   a. native and non-native phytopathogens (exogenous disturbance),
   b. altered competitive interactions due to land-use change (anthropogenic disturbance)
   c. natural succession (endogenous disturbance)

First results suggest that drought (Rebetez & Dobbertin 2004), in particular multiple drought years (Bigler et al. in press), the increasing abundance of mistletoes (Dobbertin et al. 2005, Dobbertin & Rigling submitted), some pine insects as well as some possibly pathogenic fungi (Rigling et al. 2004) and a new species of nematodes (*Bursaphelenchus vallesianus*, Braasch et al. 2004, Polomski et al. submitted) play a mutual role in pine mortality.

This thesis covers the competition part of the Pine project and deals with the hypotheses 1a, 2b and 2c. I here propose an additional hypothesis (1c), which is also a focus of my thesis:

1) c. Scots pine decline is caused indirectly by increasing competitive pressure of the possibly more drought tolerant sub-Mediterranean pubescent oak with increasing temperature.

**The concept of interspecific competition in trees**

In the main, this thesis evaluates competition between Scots pine and pubescent oak as a factor for the changing species composition at low elevations in Valais. Interspecific and intraspecific competition is involved when forests are developing towards later successional
stages. By definition, interspecific competition is “an interaction between individuals of
different species brought about by a shared requirement for a resource in limited supply, and
leading to a reduction in the survivorship, growth and reproduction of the competing
individuals concerned” (Begon et al. 1996). Trees compete for light, nutrients, water and
growing space. Species-specific differences in life history traits, such as growth form and
growth rate or the extent of shade tolerance, drought tolerance and frost resistance of saplings
and adult trees play a dominant role in the competition processes of a forest stand (Table 1).
For studying forest succession, tree species can therefore be classified with respect to their life
history strategies (Brzeziecki & Kienast 1994). Speaking in terms of Grime’s triangle, a
certain tree species can be specialised in being a good coloniser, a good stress-tolerator and/or
a good competitor (Grime 1979).

However, when it comes to trees, it is also important to examine their behaviour at different
stages of their long life, since one life history strategy may bring an advantage in the
establishment but not in the growing phase, and vice versa. In general, interspecific
competition tends to be strongest if two species show similar life history characteristics. In
cases where different species compete for the same resources but at different life stages,
interspecific competition will be lower, at least for part of the time during succession.
Moreover, if different species are not limited to the same extent by one particular resource,
and are thus partitioning the prevailing resources, coexistence will be possible (Silvertown &
Charlesworth 2001).

The strategy of a pioneer tree species favours seed dispersal and fast growth at the cost of
shade tolerance and long life, whereas the strategy of a later successional tree species gives
preference to shade tolerance as the major competitive advantage at the cost of fast dispersal
and growth. Thus, tree species often exhibit a trade-off between colonisation and competition.
At extreme sites, such as the xeric sites in Valais, tolerance of extreme climatic conditions
complicates this concept. At such sites, drought tolerance will be most important, while shade
tolerance will become less important because moisture availability limits tree size and stand
density, which consequently leads to better light conditions.

Although Scots pine is known as a pioneer tree species and pubescent oak can be seen as a
later successional tree species, a better understanding of their life history strategies is essential
for estimating the influence of interspecific competition on past and future forest dynamics. In
this thesis, different factors influencing interspecific competition were thus studied at
different levels, using a combination of dendroecological methods (chapters I, II and IV) and
forest succession modelling (chapter III) (Table 1).

Table 1. Characteristics of tree species as factors influencing interspecific competition. Left: Factors according

<table>
<thead>
<tr>
<th>Factor</th>
<th>Major parameter in the ForClim model</th>
<th>Thesis chapter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growth</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drought tolerance</td>
<td>kDrT: Drought tolerance</td>
<td>I, II, III, IV</td>
</tr>
<tr>
<td>Tolerance of nutrient shortage</td>
<td>kNTol: nitrogen tolerance</td>
<td>I, II, III</td>
</tr>
<tr>
<td>Shade tolerance</td>
<td>kLa: shade tolerance of adult trees</td>
<td>II, III</td>
</tr>
<tr>
<td>Height growth</td>
<td>kHm: Maximum tree height</td>
<td>I, II, III</td>
</tr>
<tr>
<td>Diameter growth</td>
<td>kDm: Maximum tree diameter</td>
<td>I, II, III</td>
</tr>
<tr>
<td>Stability</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Life span</td>
<td>kAm: Maximum tree age</td>
<td>I, II, III</td>
</tr>
<tr>
<td>Late frost resistance</td>
<td></td>
<td>I</td>
</tr>
<tr>
<td>Wind/Snow resistance</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reaction to damages</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Establishment</td>
<td></td>
<td>Chapter</td>
</tr>
<tr>
<td>Shade tolerance</td>
<td>kLY: light requirement of tree saplings</td>
<td>III</td>
</tr>
<tr>
<td>Regeneration potential</td>
<td>(*kLa: shade tolerance determines sapling availability)</td>
<td>III</td>
</tr>
<tr>
<td>Browsing susceptibility</td>
<td>kBrow: browsing susceptibility</td>
<td>III</td>
</tr>
<tr>
<td>Frost tolerance</td>
<td>kWiT: Minimum winter temperature</td>
<td>III</td>
</tr>
</tbody>
</table>

**Signals of competition in tree-rings**

Dendrochronologists have developed several models of tree-ring growth. Commonly, these
models contain an intrinsic (genetic structure and age), an abiotic (site conditions, such as
climate and soil) and a biotic (e.g. insects, pathogens and competition) component. Some
models emphasise endogenous vs. exogenous disturbances affecting tree growth besides
climate and intrinsic factors (cf. Cook 1990). In such a model, competition is enclosed in the
local, or endogenous disturbance component, and affects growth of individual trees either by
suppression or release.

Based on these models, dendrochronological methods have been developed to disentangle the
qualitatively different effects of age, climate and stand dynamics on tree-ring width. However,
the influence of competition has not been a strong focus of dendrochronological research so far (cf. e.g. Cook & Kairiukstis 1990, cf. e.g. Schweingruber 1996). In contrast, the influence of climate has been studied intensively all over the world (Fritts 1976, Jacoby et al. 1996, Schweingruber & Briffa 1996, Briffa et al. 2002a, 2002b). For climatological reconstructions, dominant trees are usually sampled because their growth is thought to react most sensitively to climate. However, trees that are currently classified as dominant may have been suppressed in the past (e.g. Cherubini et al. 1998), and trees with such growth patterns will therefore exhibit an unknown signal of competition besides the climate signal. It may be surprising that competition effects on the radial growth of trees have not been studied in more detail. Whether a lack of appropriate methods might be the reason for this, or the respect towards the scientific complexity of the problem, is difficult to tell. Yet, a better understanding of competition effects in tree-rings could also be useful for dendroclimatological studies.

In this context, the core part of this thesis (chapter II) aims at advancing our understanding of competition effects in tree-rings. From the concept of “allocation into structure” (Waring & Pitman 1985), diameter growth of trees can be expected to be a good indicator of their competitive status (Hanson & Weltzin 2000). According to this concept, carbon allocation to diameter growth has a relatively low priority. Even if a decrease in the competitive ability of a tree was not directly visible in changes in the production of leaves and fine roots, which have a higher priority for carbon allocation, it should therefore still be reflected in annual stem growth.

Generally, the competitive ability of a tree depends much on the crown and root space that it occupies. In this way, tree rings reflect a tree’s general level of competition, as well as annual changes in its competitive ability over time. Therefore, tree rings allow for a spatially and temporally explicit resolution of stand growth (Stoll et al. 1994). Stand dynamics can be reconstructed on the basis of living and dead trees present at the time of sampling, and changes in the competitive strength relative to that of neighbouring trees will be reflected in changes in tree-ring growth. The reaction of a tree to the death of one or several of its competitors will be visible as a growth release, i.e. suddenly wider rings. Increasing competition exerted by neighbouring trees will be visible as growth suppression, i.e. increasingly narrower rings. In chapter II, we take advantage of these characteristic reaction patterns to reconstruct stand dynamics using a dynamic competition index.
Main objective and structure of this thesis

The overall objective of this thesis was to evaluate competition and stand dynamics of mixed Scots pine and pubescent oak stands as a scientific basis for the management and conservation of these low-elevation forests in Valais. Using dendroecological methods, the autecological properties of Scots pine and pubescent oak and the competitive interactions between the two species were analysed. The results were utilised to adapt and apply a forest succession model, which contributed to identify the most important processes for future forest development.

The thesis is organised in three parts, each of which is dealing with one main issue and is concerned with a different hierarchical level (Fig. 1). The project was started at the tree-ring level (chapter I), continued at the single tree level (chapter II), and ended at the stand level (chapter III). This approach allowed me to continually integrate the results in the next higher level. In addition, the reactions of Scots pine and pubescent oak to drought were studied in more detail at the cell level (chapter IV).

![Diagram showing the hierarchy of study levels: cell, tree-ring, tree, and stand levels.](image)

Fig. 1. The thesis investigates growth of Scots pine and pubescent oak from the cell to the stand level.
Specific objectives and research questions

Autecology – Chapter I and Chapter IV

The first part of the thesis aimed at improving our knowledge on the ecology and life history strategies of Scots pine and pubescent oak for a better differentiation of the autecological requirements of the two species. We were specifically interested in the radial growth response to gradients in site conditions, such as moisture availability, soil properties and temperature (altitudinal gradient).

Dendroecological methods allow us to identify the factors that account for a large part of the variance in tree-ring growth. When studying the autecology of Scots pine and pubescent oak, we took advantage of these methods to investigate the main factors influencing tree growth close to the dry treeline. In this part, we worked with site chronologies to reveal the factors affecting average radial growth on different plots.

From the literature, the relative level of drought tolerance of the coniferous Scots pine and the deciduous pubescent oak has remained unclear. Therefore, the following specific questions were addressed: How do the trees of different plots respond to drought? Do we find species-specific patterns of drought response? How important are the available water capacity and altitude for the drought response? How drought-tolerant is pubescent oak compared to Scots pine? What are the limits of drought adaptation for both species?

Because tree-rings are the sum of the single cells produced over the growing period, reactions to drought years were also studied on the cell level to gain further insights into the species-specific mechanisms of tree-ring formation. The number and size of different cell types was related to their physiological function so as to reveal potential differences in the drought reaction of Scots pine and pubescent oak (cf. chapter IV).

The results of the autecological part provided a basis to identify the processes that are most important for the competitive ability of the two species (cf. chapter II). Furthermore, the results were used to improve the parameterisation of Scots pine and pubescent oak in the forest succession model ForClim (cf. chapter III).
Competition – Chapter II

In the second part of the project, the aim was to retrospectively trace intra- and inter-specific competition between Scots pine and pubescent oak trees over time, using a tree-ring based dynamic competition index. This novel index was developed so as to combine a spatial and a temporal component. The index was applied to evaluate how drought, past forest management and natural succession affected the competitive ability of Scots pine and pubescent oak.

Species interactions such as competition for light occur at the level of the individual, rather than the population (Huston & Smith 1987). Hence, studying competitive interactions by following individual trees throughout their life helps to improve our understanding of forest succession (Harper 1977). In this part of the thesis we used single tree-ring series of all the trees on the study plots to reconstruct the competitive dynamics of individual trees over time. A retrospective dynamic competition index was introduced, which is calculated as the yearly ratio between the basal area increment of neighbouring trees and the basal area increment of a particular target tree in the stand. The underlying idea was to remove similarities, e.g. local climate signals, in the growth patterns of single trees. The remaining dissimilarities would be called “noise” from a dendroclimatological point of view, but they should allow us to recognise the development of competitive patterns during forest succession.

The research questions addressed here were: What are the patterns of competitive ability of single trees over time? Do we find differences between the competitive dynamics of Scots pine and pubescent oak? What is the influence of historical anthropogenic disturbances and natural succession on the competitive patterns over time? Are differences in the competitive dynamics between oak and pine related to moisture availability?

The results of this chapter improved our understanding of stand dynamics in Valais, which led to a better knowledge of the most important influencing factors for forest succession and their integration in a dynamic model (chapter III).

Stand dynamics – Chapter III

The objective of the third part of the project was to reconstruct stand dynamics of xeric low-elevation forests in Valais by applying a forest gap model. The model ForClim was adapted to these rather extreme sites based on our improved understanding of the ecology of Scots pine
and pubescent oak arising from the previous chapters. The model application aimed at providing insights how past anthropogenic disturbances, such as forest grazing, may have altered the successional trajectories of these forests.

Species composition and stand structure of forests over time are often studied using forest succession models, because the long life of trees makes it difficult for an ecologist to empirically cover a sufficiently long period of real forest development. From the current stand structure, one can draw only rough conclusions on stand structures in the past, and such estimates become increasingly insecure the further back we go in time; for this reason, the retrospective index used to reconstruct competitive dynamics in chapter II was limited to 40 years.

For studying stand dynamics in Valais over a longer period, a forest succession model of the gap model type was applied. The conceptual foundations of this kind of models go back to the work of Watt (1947) on patch dynamics in forests. The death of an individual tree creates a canopy gap where regeneration takes place and the life cycle starts anew. In this conceptual model, forest stands are made up of a mosaic of gaps in different phases. The simulations with the individual-based forest gap model ForClim (Bugmann 1996) were based on our improved understanding of the autecology and the intra- and interspecific competition of pubescent oak and Scots pine (cf. chapters I, II and IV). The objective was to integrate and adapt the most important factors and the estimates of species-specific parameters to provide an adapted forest gap model that adequately reflects the complexity of forest ecosystems close to the dry treeline.

The research questions addressed in this chapter were: How have mixed stands of oak and pine in Valais developed? How relevant were past forest-use practices for the establishment of large-scale Scots pine forests at lower elevations? Has forest grazing delayed the succession towards deciduous stands? How important was pubescent oak in the past, and how important may it become in the future?

When investigating these questions, the model also served as a tool for evaluating these processes at a larger spatial scale, allowing me to draw conclusions for low-elevation forest types of Valais in general.
References


Chapter I

Radial growth responses to drought of *Pinus sylvestris* and *Quercus pubescens* in an inner-Alpine dry valley

Submitted as:
Pascale Weber¹, Harald Bugmann² and Andreas Rigling¹. Radial growth responses to drought of *Pinus sylvestris* and *Quercus pubescens* in an inner-Alpine dry valley. *Journal of Vegetation Science.*

¹Swiss Federal Institute for Forest, Snow and Landscape Research, WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland
²Forest Ecology, Department of Environmental Sciences, Swiss Federal Institute of Technology (ETH), ETH Zentrum, CH-8092 Zürich, Switzerland

Abstract

Question: Lower-montane treeline ecotones such as the inner-Alpine dry valleys are regarded as being sensitive to global change. In Valais (Switzerland), one of the driest valleys of the Alps, the large-scale low-elevation pine forests are shifting towards mixed deciduous forests. The evergreen sub-boreal Scots pine (*Pinus sylvestris* L.) shows high mortality rates, whereas the deciduous sub-Mediterranean pubescent oak (*Quercus pubescens* Willd.) is spreading. The differences in the drought tolerance between the two species are hardly known but seem to be crucial in the current processes and important to predict future forest dynamics.

Methods: We used dendroecological methods to detect species-specific patterns of growth responses to moisture. The relationship between radial growth of 401 trees from 15 mixed stands and drought was analysed by calculating response functions using yearly tree-ring indices and monthly moisture indices. Principal components analysis (PCA) was applied to the response coefficients to discover spatial patterns of drought response.

Results: The results revealed a species-specific response to moisture as well as a sub-regional differentiation of the response patterns. While the oaks showed a response mainly to the
conditions of the previous autumn and those of current spring, the pines did not start responding before May, but showed responses throughout the whole summer. Thus, oaks seem to restrict their physiological activity to periods when sufficient soil moisture is available. Moreover, the growth of pines was found to be much more dependent on prior growth.

Conclusions: Given that in Valais the climate is changing towards i) longer summer drought periods, ii) higher mean temperatures and iii) different seasonality for moisture availability, oak may benefit from being able to adapt to changing moisture conditions. In contrast, pine may increasingly face problems as it depends on summer moisture and has a smaller adaptive capacity due to its perennial photosynthetic tissue.

Keywords: climate change; dendroecology; lower treeline; Principal components analysis (PCA); response function

Introduction

Climate and the abundance of tree species

The distribution of tree species is generally determined by their ecological characteristics, i.e. by their ability to cope with the prevailing site conditions. Scots pine (*Pinus sylvestris* L.) is known as the most widely distributed conifer, covering the whole Euro-Sibirian range (Meusel et al. 1965). Pubescent oak (*Quercus pubescens* Willd.) is a typical sub-Mediterranean broad-leaved tree, with a much smaller ecological range (Meusel et al. 1965).

In Valais, an inner-Alpine dry valley in the southwest of Switzerland (Fig. 1), the ranges of both species overlap, and oak and pine form mixed stands at altitudes up to 1200 m a.s.l. These forests are mainly found near the forest-steppe ecotone and constitute the lower xeric treeline. The current forest stands have developed under changing anthropogenic and natural disturbances, as well as with natural succession. The coexistence of pine and oak is partly a result of past forest management, such as goat grazing, timber harvesting and the selective withdrawal of forest products. All these anthropogenic disturbances favoured the early-successional pine forest associations, which still cover a large part (approx. 12,000 ha) of the low-elevation forests in the Valais. But these management activities have been abandoned,
particularly in the second half of the 20th century. For this reason, oaks now benefit from less heavy browsing by goats (Gill 1992, Mayer et al. submitted), reduced harvesting and better regeneration conditions. As a more late-successional species, oak is capable of competing against the pioneer pine species, which consequently suffers stronger suppression.

Until the 1980s, pine decline in Valais was thought to be related partially to fluorine emissions originating from the aluminium industries (Flühler et al. 1981, Kienast 1982, Kontic et al. 1986). However, the installation of filters stopped pollution, and today the trees do not any longer show pollution symptoms (Rigling & Cherubini 1999). Furthermore, the areas currently showing the highest mortality rates (Rigling, unpublished data) do not correspond to the historically most polluted areas (Flühler et al. 1981).

During the past decades, the successional processes described above have coincided with climate warming (Begert et al. 2005). Since 1980, the number of days per summer with a mean temperature above 20° C has more than doubled (Rebetez & Dobbertin 2004). Degree-day sums play an essential role in determining the length of the vegetation period (Menzel & Fabian 1999, Defila & Clot 2001) and in modifying the development and the abundance of insect populations (Ayres & Lombardero 2000, Bale et al. 2002), phytopathogens (Paine et al. 1997, Lieutier et al. 2004) and mistletoes (Iversen 1944, Dobbertin et al. 2005), which are three factors potentially causing pine decline. Increasing temperatures are assumed to lead to increasing drought by boosting evapotranspiration. Additionally, in the last 60 years there has been a shift in the seasonality of water availability in Valais (Fig. 2). This may cause adaptive problems for some tree species. Overall, it seems likely that it is a combination of the anthropogenic, biotic and abiotic factors mentioned above that has led to the high mortality rate of pine. The relative contribution of each single factor, however, is poorly known.

Due to changes in both land use and climate, a shift in tree-species composition is becoming apparent in the low-elevation forests in Valais. The spread of oaks and the locally high mortality rates of pine allow us to estimate how fast these forest changes may be. Indeed, a remarkable change from pine towards deciduous tree species has recently been reported. Between 1983 and 1993, the stem numbers of pubescent oak (+30%) and birch (Betula pendula Roth) (+27%) have increased, while the stem number of Scots pine (-6%) has decreased (WSL 2001). The repetition of up to 70-year-old vegetation records showed that there has been a significant change towards oak in 30% of the relevées (Kienast et al. 2004).
Forest ecotones such as the lower-montane treeline are regarded as sensitive to global change (Hansen & di Castri 1992), with consequences ranging from the species to the landscape level (Penuelas & Filella 2001, Theurillat & Guisan 2001, Walther 2002, Penuelas & Boada 2003). Drought-induced shifts in vegetation distribution are expected to be most rapid in semi-arid landscapes (Allen & Breshears 1998). For an estimate of the future growth performance of pine and oak in Valais and other inner-Alpine dry valleys from where comparable processes are reported (Vertui & Tagliaferro 1998), the capacity of species to tolerate increasing drought will play an essential role.

**Growth responses to climate**

Tree growth is influenced by both external and internal factors. Many dendrochronological studies have shown that the external factor climate normally explains a relatively large part of the temporal variability in tree-ring width (Fritts 1976, Jacoby et al. 1996, Schweingruber & Briffa 1996, Briffa et al. 2002a, 2002b). At the upper treeline, growth rates contain a strong temperature signal, because temperature mainly limits tree growth in cool-moist climates; whereas at the lower (xeric) treeline, the availability of moisture has a considerable impact on tree growth (Fritts 1976, Lamarche 1978).

In general, Scots pine and pubescent oak are known to be relatively well-adapted to drought (Ellenberg 1986). As a light-demanding pioneer, pine is widely distributed and thus is not highly specialised with respect to site conditions. Pine has evolved to avoid competition from other tree species by being capable of growing in extreme conditions, although Pinaceae are reported to be comparatively vulnerable to xylem embolism at xeric sites (Cochard 1992, Martinez-Vilalta et al. 2004). The sub-Mediterranean deciduous oak has evolved physiologically to adapt to drought e.g. by developing a low water potential threshold for stomatal closure, osmotic adjustment, xeromorphic leaves and a deep rooting system (Epron & Dreyer 1993, Abrams 1996, Timbal & Aussenac 1996). Thus it seems that the evergreen pine and the deciduous oak pursue quite different ecological strategies of adaptation and survival, and one would expect pine to react differently to the drought regime in an area such as the Valais compared to oak.

Several studies have investigated the ecological effects of climatic conditions on the growth of Scots pine and pubescent oak at xeric sites using the method of response function analysis.
(Serre-Bachet 1982, Tessier 1986, Kienast et al. 1987, Tessier 1989, von Lürthe 1991, Tessier et al. 1994, Oberhuber et al. 1998, Rigling et al. 2001). Even though such investigations do not directly measure physiological constraints, the interpretation of the dendroecological results can contribute to our knowledge about the autecological characteristics of a certain tree species. Compared to physiological investigations, which are usually short-term, dendroecology allows us to retrospectively analyse climate-growth relationships over long periods. However, until now most dendroecologists studying Scots pine and pubescent oak have used temperature and precipitation data as explanatory variables, rather than calculating a moisture index, although the latter would make it easier to arrive at a functional interpretation of the results.

In this study, we analyse the influence of drought on the growth performance of Scots pine and pubescent oak along several altitudinal gradients with differing site conditions in Valais. The aim is to estimate quantitatively and qualitatively the influence of drought on the growth of pine and oak. The research questions are whether we can identify (1) a species-specific drought response, and (2) an altitudinal gradient in the response to drought. Finally, we will evaluate the implications of the differences between the two tree species in the context of climate and land-use change.

**Materials and Methods**

**Study sites**

The Valais is an inner-Alpine dry valley situated in the southwest of Switzerland (Fig. 1, Sion, 46°13’40” N, 7°21’35” E). The climate in the Visp region is fairly continental (annual mean temperature [Tmean] = 8.6 °C, annual precipitation sum [Psum] = 599 mm, Psum_{June-August} = 123 mm, Gams Index of Continentality (Gams 1932) = 47; all data for the norm period 1961-1990). However, the Sion region, being closer to the humid air coming from Lake Geneva, is less continental (Tmean = 9.2 °C, Psum = 598 mm, Psum_{June-August} = 155 mm, Gams Index of Continentality = 39; again, norm period 1961-1990). In 2003, the measured mean temperatures from the beginning of April to the end of October varied between 14.9 °C and 16.5 °C for the 15 study plots (T_{2003}, Table 1). These means provide a rough indication of the between-site differences in the prevailing climatic conditions.
Because of the dry climate (Braun-Blanquet 1961, Ozenda 1985) and the steep slopes, the soils are generally not well developed. Soil types were classified based on the FAO (1998) nomenclature using a soil profile at each of the 15 sampling plots (Table 1). The soil types determined were Regosols, Rendzic Leptosols and Distric Cambisols. On xeric sites, soil type plays an important role for determining the available water capacity (AWC). AWC was thus estimated for each plot using data on soil texture, bulk density, content of coarse fragments, and depth of each of the recorded soil horizons according to AG Bodenkunde (1982). With values below 120 mm, most of the plots exhibit low to very low AWCs (Table 1).

Table 1. Site characteristics of the 15 sampling plots. T2003 = measured mean temperature for April-October 2003. AWC = available water capacity of soils. Age, dbh (diameter at breast height), height: mean of the 10 tallest pine/oak trees.

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<th>Soil type (FAO)</th>
<th>AWC [mm]</th>
<th>Age [yr] (pine/oak)</th>
<th>Dbh [cm] (pine/oak)</th>
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<td>23.3 / 17.7</td>
<td>12.6 / 10.9</td>
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</table>

In this study, we focused on forests below the upper distribution limit of pubescent oak, i.e. below 1200 m a.s.l., that have been described as pine forests belonging to the Ononido-Pinetum, Odontito-Pinetum and Erico-Pinetum associations (Schmid 1936, Plumettaz Clot 1988), with different species composition and structure depending on aspect, elevation, soil type and past forest management.

To analyse the relationship between site conditions and the growth of pine and oak, five locations were selected in the Valais (Fig. 1), and at each location three study plots were selected along an altitudinal gradient (Tab. 1). The five locations were selected so as to include some fairly extreme climatic conditions in the Valais. Each of the gradients extended
across continuous forest with similar stand conditions and consisted of three mixed pine/oak plots, preferably with altitudinal differences between the plots of more than 150 m. Three of the gradients were facing south, one east and the lowest west. They usually started just above the vineyards, i.e. between 590 and 950 m a.s.l., and ended at 930-1200 m a.s.l., where the proportion of oak decreases markedly and spruce (*Picea abies* Karst.) starts to occur more frequently. All sampling sites were characterised by steep slopes with an inclination of 93% to 162%, and they differed not only in aspect and altitude, but primarily in their microclimate and soil type (cf. Table 1).

![Map of the inner-Alpine dry valley Valais](image)

**Fig. 1.** Map of the inner-Alpine dry valley Valais: 5 altitudinal gradients consisting of 3 single plots each at Eschwald, Eggerberg, Salgesch, Lens and Bramois (black arrows), climate stations at Sion (482 m a.s.l.) and Visp (640 m a.s.l.) (grey triangles).

**Data collection and analysis**

On each of the 15 sampling plots of 12 m radius, all the trees were cored using an increment borer in summer 2002. Two cores were taken at breast height for standard dendrochronological analysis, and one core was extracted at the stem base to determine tree age. For each tree, height, diameter at breast height (dbh) and social class (dominant, codominant, subdominant, or suppressed) were recorded. The sampling was designed so as to include trees of all social and age classes.
Tree-ring widths were measured with a Lintab3 measuring system (F. Rinn S.A., Heidelberg, Germany) using the TSAP tree-ring software Version 3.5 (Rinn 1996). At these rather extreme sites, a few cores had to be excluded from further analyses because of very suppressed growth with rings that were not detectable unequivocally. Crossdating was done both visually and using standard techniques (Fritts 1976, Cook & Kairiukstis 1990). A few missing rings due to dry years had to be inserted in the pine series. The cross-dating was verified statistically by using the TSAP and the COFECHA routines (Holmes 1994).

By applying the interval sign test of TSAP, the series with a percentage of agreement (Gleichläufigkeit) (Eckstein & Bauch 1969) above 60% were selected for further analysis. Between 11 and 53 series per species and plot conformed to our requirements (Table 2). Differences in the number of available tree-ring series between the plots were caused mainly by the varying presence of young or suppressed trees on the sampling plots and by altitudinal effects (fewer tall oaks at higher elevations).

Mean standard and residual chronologies were produced using the ARSTAN software (Cook 1985, Holmes 1994). In a first step, the variance of each ring-width series was stabilized by a power transformation (Cook & Peters 1997). In a second step, the series were standardized by fitting a cubic-smoothing spline with a 50% frequency response of 128 years (Cook & Peters 1981) mainly to exclude the age effect. By subtracting the expected values given by the spline function from the power-transformed values, indexed series were produced and finally averaged to 15 pine and 15 oak standard chronologies (STD) by a robust biweight mean (Fritts 1976, Cook et al. 1990). Residual chronologies (RES) were calculated based on autoregressive modelling.

For quality control, basic chronology statistics (Fritts 1976, Briffa & Jones 1990) such as mean rbar, mean sensitivity and expressed population signal (Wigley et al. 1984) were computed for all the RES chronologies for the period 1950-2001 using ARSTAN.

**Climate data**

Precipitation data from the two regional SMI (Swiss Meteorological Institute) climate stations of Visp and Sion were used (Fig. 1). Temperature series as long as 50 years were only available for the station at Sion. Because the location of the station was moved in the 20th
century, the climate series for both temperature and precipitation had to be corrected using nearby “bridging” stations and were homogenized as described in Bigler et al. (in press).

As we were interested in the functional reaction of tree growth to climate, we used a moisture index (Ppot) (Bigler et al. in press) – the difference between precipitation and potential evapotranspiration according to Thornthwaite (1948) – for the statistical analyses. In a pilot-study with other ecologically based indices such as monthly mean temperature, monthly precipitation sum, length of summer drought periods and minimal temperature of April and May (late frost), the index Ppot showed the highest correlations with tree-ring growth. This moisture index gives a better estimation of water availability for trees than precipitation data, since it captures the joint effects of temperature and precipitation. Another advantage of calculating a combined index is that interpretation problems due to the inverse effects of temperature and precipitation can be avoided (Fritts 1976).

The annual courses of the moisture index Ppot illustrate the typical moisture deficit in summer for the climate stations of Visp and Sion (Fig. 2).

Fig. 2. Mean yearly course of moisture index Ppot (= Precipitation - Potential Evapotranspiration, Thornthwaite 1948) for three periods in the 20th century. Both moisture regimes show a dry period from May to September.

Both stations show the tendency of a change in seasonality during the 20th century. Between 1941 and 2001, the moisture availability showed a significant positive trend in March (Visp: p < 0.05, Sion: p < 0.05) and May (Visp: p < 0.1); on the other hand, moisture availability in August (Visp: p < 0.05, Sion: p < 0.01) decreased significantly.
**Statistical analysis**

We used response functions, i.e. a multiple regression after extracting the principal components of the climatic predictors, to evaluate the differences in the reaction of pine and oak to climatic influences. In this way, we avoided the limitations of simple correlations, which may be difficult to interpret due to inter-correlations within the climate data (Fritts 1976, Guiot et al. 1982, Fritts & Guiot 1990). The analysis was performed with the routine PRECON (Fritts et al. 1991) with the RES chronologies as dependent variable, including monthly moisture availability (Ppot) from June(0-1) of the preceding year to September(0) of the current year of growth as independent variables. The data of the climate station at Visp were used for Eschwald and Eggerberg, and the climatic data of Sion were used for Salgesch, Lens and Bramois (Fig. 1). Most plots were located in a distance less than 5 km from the climate station used, except for the plots of Salgesch with a distance of approx. 20 km to the climate station of Sion. As most of the tree-ring chronologies covered at least the last 50 years, the period of 1950-2001 was chosen for the analyses. The principal components whose cumulative eigenvalue product (CEP, sometimes also abbreviated as PVP) was >1 were selected for the regression (Guiot et al. 1982), and in a bootstrap procedure 100 iterations (Guiot 1982, 1990, Fritts et al. 1991) were calculated to estimate the standard deviation of the response coefficients. The ratio between the response coefficient and its standard deviation was used to estimate the significance of the response (z-test). The influence of prior growth compared to climate was evaluated for all the STD chronologies by recalculating the response functions, including the values from the STD chronologies up to a lag of −3 years as independent variables.

Two procedures were established to evaluate the species-specific and the regional response patterns. First, the relationships between moisture availability and tree growth were summarised over all the plots and for the two species separately by recording the percentage of plots exhibiting a significant relationship on the 95% confidence level for each month. The significance of the difference in the response between oak and pine was then tested by a chi-square test of independence (Sokal & Rohlf 1995). Second, regional response functions were calculated based on regional average tree-ring chronologies.

Finally, the 16 monthly response ratios of all the plots were introduced into a Principal components analysis (PCA) (Tessier 1986, 1989) using the statistic software R (R
Chapter I

Development Core Team 2003) to detect the relationships between the response functions of the different sites and species. The ordination axes are linear combinations of the monthly responses. By applying this method, groups of similar response function patterns were formed and the main grouping factors were identified.

Table 2. Characteristics of tree-ring chronologies: N of cores, N of trees, maximum, mean and minimum age at coring height, mean radial growth (\( G_{\text{mean}} \)) and its standard deviation (\( G_{\text{std}} \)), cross-correlation between single series (mean \( r_{\bar{b}} \)), mean sensitivity of single series (mean \( S \)) and expressed population signal (eps) of the residual chronologies of all 15 plots for oak and pine. Grey: data sets of limited quality.

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<th>N trees</th>
<th>Max. age</th>
<th>Mean age</th>
<th>Min. age</th>
<th>( G_{\text{mean}} ) [mm]</th>
<th>( G_{\text{std}} ) [mm]</th>
<th>mean ( r_{\bar{b}} )</th>
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Results

*Characteristics of the tree-ring chronologies*

For each plot, separate chronologies were produced for both pine and oak. The statistical parameters document that the chronologies are generally of good quality (Table 2). In five chronologies, the number of trees was lower than 10, but this affected the quality only in the case of the chronology egc (6 trees) (expressed population signal (eps) < 0.80). The low age of the trees of egb (oaks only), leb and bra (both species) caused some problems in the further analyses because of the chosen calculation period of 1950-2001. To guarantee the comparability of the results, the chronologies of leb and bra were thus not used in the response function analyses, and therefore response functions of 13 plots will be presented only.

*Single-plot response to moisture*

On all plots, the growth of both tree species was positively correlated with moisture for most months of the period of interest (June to September) (Fig. 3). Separating the single chronologies’ response functions in the Visp and the Sion region resulted in a regional differentiation of the patterns (Fig. 3). In the more continental climate of the Visp region, pine and oak showed a more distinct seasonal response pattern than in the Sion region. Furthermore, the single-plot response patterns of the Visp region tended to be more similar to each other than those of the Sion region. Only the oaks of the high-elevation plot egc (1200 a.s.l.) deviated considerably from the general course. Their responses were lower in November, February and March.

The differences between the two regions were also visible in the response curves of the regional average chronologies for Visp and Sion (Fig. 3). The oaks of the Visp region responded most strongly to moisture in autumn of the previous year, whereas the oaks of the Sion region showed the strongest response to May and June moisture. The Visp pines showed significant responses in their growth dating back to August and November of the previous year and had a continuous response during the summer months (June-August) of the current year. In comparison, pines of the Sion region had a peak in their response to moisture in May.
Fig. 3. Response function coefficients for 13 oak (left) and 13 pine (right) chronologies from June of the previous year to September of the current year. The response function was calculated with yearly tree-ring width (residual chronologies) as the dependent and monthly moisture indices Ppot as the independent variables for the period 1950-2001. Regional responses (meanvisp, meansion) were calculated from the regional average chronologies. Significances of the regional responses are given: a = p < 0.001; b = p < 0.01; c = p < 0.05.

Looking at the significances of the single-chronology responses, the reaction of the oaks was notably more distinct than that of the pines (Table 3). Within the oak chronologies, available soil water on the plots (AWC) acted as a sorting criterion for the response patterns. The oaks growing on soils with a low available water capacity (AWC = 36-46) tended to respond to moisture in the autumn of the previous year, while the oaks growing on slightly better soils (AWC ≥ 47) responded mainly from March_{0} to June_{6}. With the pines, no main sorting factor was evident among elevation, AWC, T_{2003}, maximum tree age and tree height.
Table 3. Significance of responses to moisture index Ppot, for 13 plots, a) for oak, b) for pine and the overall explained variance by climate. Chronologies are sorted according to the available water capacity of the soil on the plot (AWC).

a) Quercus pubescens

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b) Pinus silvestris

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|----------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---------------------|
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| 37 esc | << | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | 0.59 |
| 41 ega | * | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | 0.67 |
| 46 esa | * | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | 0.54 |
| 47 brh | * | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | 0.63 |
| 61 saa | << | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | 0.51 |
| 69 egf | * | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | 0.54 |
| 73 lec | * | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | 0.49 |
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| 83 egc | * | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | 0.50 |
| 91 lea | * | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | 0.55 |
| 97 sab | * | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | 0.61 |
| 114 brc | << | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | @ | 0.44 |

Level  | significantly positive oak, pine | significantly negative oak, pine |
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Differences in the response to moisture between oak and pine

The percentage of significantly responding chronologies was calculated for every month to emphasize the different response patterns of the two species (Fig. 4). Months with significant responses of a large percentage of chronologies indicate a species-specific reaction to moisture. Significant differences in positive response between the two species were identified in August, September and October of the previous year and in April and July of the current year. Unlike the pine chronologies, 38% to 62% of the oak chronologies responded in a
significantly positive manner to moisture in the previous autumn (September-November). During winter (December-February), the response of both species was low. In early spring, oak already recorded positive responses on a high level starting in March (38%), with a peak in April (62%). In comparison, pine showed no high responses until May (54%), but remained responsive throughout the summer. In July, when 23% of the pine chronologies were still responding, the response of oak dropped to 0%. 54% of the pine chronologies, but none of the oak chronologies, responded in a significantly negative manner to the conditions in June of the previous year.

Fig. 4. Summarised growth response to the monthly moisture index Ppot. Percentage of chronologies with a significant (\(p < 0.05\)) negative or positive response of pines and oaks from June to September are shown. 100% = 13 chronologies. Circles indicate significant differences in the responses between oak and pine (\(p < 0.05\)).

Groups of similar response patterns

The first three axes of the principle components analysis (PCA) explained 46.3%, 12.5% and 10.7% of the total variance (69.5% altogether). The ordination of the first two components resulted in a nearly complete separation of oak and pine (Fig. 5). However, all the chronologies had negative loadings on the first component axis, indicating that the trees were partly affected in a similar way by water availability. On the second component axis, the oaks were located mostly in the positive, and the pines mostly in the negative part. The main dividing months in the positive direction were December (7) and April (11). In the negative direction, the main loadings were July (2), August (3) and July (14).
Within the ordination of components 2 and 3, the division into subgroups of similarly responding chronologies was even more apparent (Fig. 6). Most of the pine chronologies were grouped according to the response in summer of both the previous and the current year. The oak chronologies of Eschwald were principally associated with a response to the moisture conditions of the previous autumn. The rest of the chronologies made up a less pronounced group, related to winter and spring responses.

Calculating the PCA for oaks and pines separately (Fig. 7) revealed site-specific response patterns. For both species, the PCA split the response into the two regional groups of Visp (Eschwald, Eggerberg) and Sion (Salgesch, Lens, Bramois). The Eschwald sites, making up a narrow group of arrows, were found to be different from the other sites for both species. In oaks, the discrimination of the plots was related to the soil AWC. No altitudinal gradient in the response was visible.
Influence of prior growth

The response functions were also calculated for all the STD chronologies to detect the parts of variance in tree-ring width explained by climate and by prior growth. Overall, the total explained variance was high in both species but tended to be higher in pine than in oak, although this difference was not significant (Fig. 8). However, climate explained significantly more variance in tree-ring width of oaks than of pines (p < 0.05). On the other hand, prior growth was significantly more important in pines than in oaks.

Fig. 7. PCA with response ratios to moisture index Ppot for oak (left) and pine (right) (second and third component axes). Eschwald and Eggerberg belong to the Visp region, Salgesch, Lens and Bramois belong to the Sion region. Numbers 1-16 stand for the months from June$_{n-1}$=1 to September$_{n-1}$=16; January$_n$=8. AWC = available water capacity of soil.

Fig. 8. Notched boxplot of explained variance in the response functions of oak and pine. If the notches of two plots do not overlap, the medians are significantly different (p < 0.05). Response functions of STD chronologies, including the STD chronologies up to a lag of -3 years as independent variables. N=15 for each oak and pine.
Discussion

Species-specific response to moisture

Our results consistently indicated a species-specific seasonal differentiation of the response to moisture availability. These differences can be interpreted in the context of the ecological differences between a sub-boreal (pine) and a sub-Mediterranean (oak) tree species. The summarised response patterns of pine and oak (Fig. 4) illustrate the differences best and can be interpreted in terms of ecophysiological adaptations to the extreme site conditions in the Valais, as follows.

Oaks in general responded positively to the moisture of all the autumnal months (September, October, November) of the preceding year, whereas pines showed positive responses mainly in previous August and November (Fig. 4). Growth relations to climate in August have been reported from various studies with conifers (Fritts 1974, Gutierrez 1991, Graumlich 1993, Oberhuber et al. 1998, Oberhuber & Kofler 2000, Rigling et al. 2001, Tardif & Stevenson 2001, Rigling et al. 2002, Rigling et al. 2003, Takahashi et al. 2003). Takahashi (2003) interpreted this result for Abies veitchii by bud formation for the next year, which depends on the amount of sugars available at this time.

Besides this predisposition regarding the amount of new photosynthetic tissue for the next growing season, the photosynthetically active tissue remaining from the previous years has to be considered in evergreen species such as pine. Needle loss following drought stress (Pouttu & Dobbertin 2000) leads to a smaller photosynthetic capacity in subsequent years. As a result, the growth of pine was found to be much more dependent on prior growth than that of the deciduous oak (Fig. 8). Thus, this lag effect, which is characteristic for evergreen coniferous tree species in temperate climates, can obscure the response of pine to current moisture conditions. In Valais, longer periods of drought (multiple drought years) are apparently causing reduced needle mass in pines (Pouttu & Dobbertin 2000) and considerable growth decreases followed by a higher mortality risk (Bigler et al. in press).

Apart from differences in the response to the conditions of the preceding year, our results pointed to potential differences in the start of the growing season between pine and oak (Fig. 4). The start of the growth response of oak in March can be interpreted as the production of new water-conducting tissue, when drought normally is not limiting yet (Fig. 2). Moreover,
the first differentiated earlywood cells are rapid hydraulic conductors (Abrams 1990), transporting the water to the crown and promoting bud break (Nardini 2002). In Central European Quercus petraea, earlywood vessels were found to be established already by the end of April (Breda & Granier 1996). In contrary, the rather late start of the response of pine in May, when dry conditions already occur (Fig. 2), could have implications for the pine’s further growth performance. In fact, it is known that wood formation in oaks at Visp started in the second half of April, around 3 weeks earlier than in pines, in the year 2002 (Zimmermann & Cherubini, unpublished data).

In the driest month, July, when the oaks showed no significant response at all (Table 3, 5% significance level), the 3 pine chronologies of the plots with the lowest water-holding capacities responded significantly to moisture. As an adaptation to summer drought, the oaks probably show a summer stop of activity, which is typical for Mediterranean species (Cherubini et al. 2003) and allows them to avoid cavitation (Tyree & Cochard 1996, Lebourgeois et al. 1998, Nardini & Pitt 1999). The physiological activity of pines in July, however, probably induces drought stress, which increases the risk of cavitation. Among conifers, pines were found to be quite vulnerable to drought-induced xylem embolism (Martinez-Vilalta & Pinol 2002, Martinez-Vilalta et al. 2004).

According to the PCA (Fig. 5 and 6), the chronologies can be grouped well into summer, winter/spring and autumn responders. Pines are mostly summer responders. July is the driest month in the year and therefore drought stress is frequent. Because pines start responding late in the year (not before May), they appear to be dependent on summer moisture to grow a wide ring and to produce enough carbon reserves. Our results suggest that oaks are autumn- or winter/spring-responders. As a sub-Mediterranean tree species, pubescent oak is adapted to summer drought. As a consequence, the oaks concentrate their activity on those periods when moisture conditions are most favourable, i.e. during autumn, winter and spring.

The positive response to winter conditions of a deciduous species may appear surprising, but we see two ways to interpret this phenomenon. First, winter precipitation is needed to refill the soil with water for the next growing season. This effect of moisture availability in winter would thus be indirect, because deciduous trees do not normally take up much water until they start photosynthesis in spring. Second, winter moisture can have a direct positive effect on root growth. Root growth in winter may be advantageous in summer-dry climates
(Cherubini et al. 2003). Oaks have been reported to grow fine roots even in winter, given that soil temperature is above 0 °C (Hoffmann 1974, Teskey & Hinckley 1981). Mean monthly soil temperatures below 0 °C are exceptional for Sion and Visp (Defila & Brändli 1989), and therefore root growth in winter is at least conceivable. Root growth in the pre-season can be particularly relevant for young trees (as many of the oaks in our sample are), because they still need to enlarge their root systems (Aussenac & Valette 1982).

Generally, frost is a key factor for the distribution of pubescent oak, a species that is restricted to the sub-Mediterranean area, and in the Valais to elevations below 1200 m a.s.l. (Burnand 1976). Because of their ring-porous wood anatomy, oak species are susceptible to winter and spring frosts (Cochard & Tyree 1990, Thomas et al. 2002), and oak seedlings have been found to be particularly damaged by late frost (Chaar & Colin 1999). Thus, oak regeneration is limited to lower elevations. Lower growth rates and less regeneration at higher elevations (Mayer et al. submitted) could explain that we found the oaks were smaller, thinner and younger at higher altitudes, whereas the pines were older and thicker at higher altitudes (Table 1). Thus, higher temperatures due to climate change may shift oak distribution to higher altitudes also for this reason.

**Regional differentiation**

Instead of the expected altitudinal differentiation of the response to moisture availability, our investigations revealed mainly a sub-regional differentiation in the Visp vs. the Sion area (Fig. 7). In the drier climate of the Visp area, both species were similar in having a more pronounced response to moisture than in the less continental Sion area (Fig. 3, Table 3).

In both species, the gradient of Eschwald was clearly distinguishable from the other gradients (Fig. 7). Its unique position can be explained by the combination of site factors such as 1) very dry soils in summer due to low water holding capacity, 2) the continental dry climate of the side-valley, and 3) the eastern aspect. The characteristic autumn response of oaks at Eschwald can be interpreted physiologically. Trees growing on soils with such low water-holding capacities are limited by drought occurring in the period from spring throughout the whole growing season. They thus adapt a strategy to prepare for the growing season in the previous autumn. These preparations may include the storage of metabolic compounds as well as root growth.
Interestingly, the gradients near Sion (Salgesch, Lens and Bramois) were not separated clearly from each other for either species (Fig. 7), even though Bramois is situated on the northwest-facing slope and both Salgesch and Lens on the south-facing slope. As the gradient of Bramois was located at a lower elevation, we conclude that 200 m in altitude probably compensated for the northwest aspect. In contrast to the gradients of Eschwald and Eggerberg, the soils of the plots around Sion were characterized as rendzic leptosols (except for brb, which was a calcaric cambisol, Table 1). While they all had free carbonate in their top soils, the soils at Eschwald and Eggerberg were partly decarbonated or carbonate free on silicate. The similarity of the soil types in the Sion area, combined with the presented grouping of the response patterns of this sub-region, suggests that nutrient and water availability in the soil may be a differentiating factor for tree-growth patterns on xeric sites in Valais. For oaks, it seems that the soil type is an important factor for dividing the response patterns into spatial subgroups. This is also visible from the ranking of the significant responses by AWC (Fig. 7, Table 3).

In conclusion, in both species the sub-regional differentiation was mainly caused by different responses to differing climatic and soil conditions. By using the “closest to real” climate data from the two climate stations of Visp or Sion, we obtained the most accurate response patterns (Tessier 1989). In this sense, for each plot using the climate data of the closer of the two stations was not the reason for the sub-regional differentiation in the first place.

**Implications for climate and land-use change**

According to Rebetez and Dobbertin (2004), increasing drought due to climate change will lead to increasing pine mortality in the Valais in the future. Increasing temperatures and a change in the seasonality of precipitation towards a more Mediterranean climate with extended summer droughts (Fig. 2) will modify the response patterns of oak and pine to moisture availability. On the one hand, oaks may benefit from increasing moisture in spring and autumn (Fig. 4). On the other hand, pines may benefit in May, but are likely to suffer with increasing drought in August (prior and current year). A comparable study of *Quercus petraea* and *Quercus robur* in Germany found a shift in the response to winter precipitation, which was explained by a changing climate (von Lürthe 1991). In contrast, Solberg et al. (2002) observed a shift in the response patterns of *Picea abies* in Norway, where the response to winter precipitation was decreased by a stronger oceanic influence due to climate change.
Moving response functions (Biondi & Waikul 2004) could be applied for the Valais to longer chronologies than ours to detect a possible shift in the response pattern.

Our results imply that oak is better able to adapt to a changing climate regime with longer summer droughts than pine. Oaks and pines in a Mediterranean forest in the southwestern part of France showed similar differences in their adaptability (Tessier 1986). In a study by Fekedulegn et al. (2003) in the Appalachian mountains, the adaptive capacity to drought of individual Liriodendron tulipifera L. trees was interpreted as depending also on their root:shoot ratio, besides the species-specific growth strategy. By analogy, many pine trees that have grown up under earlier, cooler conditions may face considerable problems in a warmer and drier climate, because their root:shoot ratio may not be adapted to the conditions prevailing today and in the future. Likewise, problems with a changing water regime were recorded for formerly irrigated pines in the Valais (Rigling et al. 2003) and for pines on a sinking groundwater table in Germany (Wirtz 2002).

Single (Kienast et al. 1987, Schweingruber 1990) and multiple drought years (Bonn & Worbes 1991, Bigler et al. in press) can play a very important role in influencing the species composition in forest ecotones, such as the one studied here close to the xeric, lower-montane treeline in the Valais. Besides the inter-annual variability of moisture, the intra-annual variability of moisture, i.e. the seasonality of moisture (Fig. 2) and the length of single drought periods (Kuhn 1973, Bigler et al. in press), contributes to determining radial growth, and has to be considered as well.

Furthermore, the historical and still ongoing changes in the forest management mentioned in the Introduction are altering the competition regime and will consequently change the growth regime at the individual tree level as well. Lower thinning intensities, for example, increase root competition and may thus further decrease the drought resistance of the trees (Sabate et al. 2002, Misson et al. 2003a, Misson et al. 2003b).

In Valais, many factors linked to climate and land-use change potentially affect the mortality rates of pines (Rigling & Cherubini 1999, Rigling et al. 2004). This study has revealed that summer drought has a strong impact on the growth performance of pines. As a consequence, growth imbalances (lower storage of carbon reserves, needle loss) and a limited adaptive capacity may finally lead to a high mortality risk for these trees (LeBlanc & Foster 1992,
Our results suggest a more flexible reaction and therefore higher drought resistance of oak than of pine. Whether the difference in drought response will finally change the competition regime between oak and pine in Valais will be the subject of future research.

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Radial growth responses to drought


Radial growth responses to drought


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Chapter II

Using a retrospective dynamic competition index to reconstruct forest succession

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¹Swiss Federal Institute for Forest, Snow and Landscape Research, WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland
²Forest Ecology, Department of Environmental Sciences, Swiss Federal Institute of Technology (ETH), ETH Zentrum, CH-8092 Zürich, Switzerland
³WSL, Sottostazione Sud delle Alpi, Via Belsoggiorno 22, CH-6504 Bellinzona-Ravecchia, Switzerland

Abstract

1 Understanding forest dynamics and stand structures is crucial for predicting forest succession. However, many forests have been altered due to century-long land-use practices, which complicates the reconstruction of past and current successional trajectories.

2 For a better knowledge of successional processes, we suggest studying the intra- and interspecific competition among single trees over time and use mixed Scots pine (Pinus sylvestris L.) and pubescent oak (Quercus pubescens Willd.) stands in the inner-Alpine dry-valley Valais as a model system. The aim is to analyse current stand structures in terms of recent changes in the competitive interactions at the single tree level and to relate these competitive dynamics to land-use change and increasing drought due to climate change.

3 We introduce a tree-ring based competition index to reconstruct the competitive dynamics of individual trees over time. This new retrospective dynamic competition index combines a temporal and a spatial component by calculating the yearly ratio between the basal area increments (bai) of the neighbouring trees and the subject tree. On five whole-stand plots, the position of 456 trees was recorded and increment cores were taken to derive bai data. The individual dynamic competition curves were aggregated in clusters of similar competitive patterns for both tree species.
The trees were clustered into a large group of trees with constant competition over time. However, a smaller group of pines had recently faced increasing competition. In addition, stand structure analyses indicated a change towards a higher proportion of oak. This change in the competitive ability between oak and pine was found to be related to drought, in that oak had a competitive advantage in dry years. Furthermore, the high proportion of dead branches of the pines with decreasing competitive abilities indicated increasing competition for light as a consequence of natural development towards a later successional stage that favors the more shade-tolerant oak.

The new retrospective dynamic competition index proved to be promising in studying the succession of forests. The method allows us to identify changes in the competitive ability of single trees with a high temporal resolution and without repeated assessments and is therefore valuable for forest succession studies.

Keywords: climate change; competition index; dendroecology; forest succession; land-use change; individual trees; Quercus pubescens; Pinus sylvestris; Valais

Introduction

Intra- and interspecific tree competition is an important factor in forest succession. By definition, competition is “an interaction between individuals, leading to a reduction in the survivorship, growth and reproduction of the competing individuals concerned” (Begon et al. 1996). In forest succession, competition is assumed to play a major role in species replacement (Bazzaz 1996). Disturbance is viewed as a mechanism for initiating succession (Bazzaz 1996) and can have a long-term effect on stand development and successional pathways (Oliver & Larson 1996) by changing competitive dynamics among trees. When predicting future forest development, reconstructing past disturbance regimes and identifying changes in competitive interactions are key issues. Understanding the dynamics of forest stands with strong past anthropogenic disturbances is particularly difficult because the different types of human impact typically vary in time and space.

Many forests have been altered over centuries by historical land-use practices. However, for economic reasons, a large part of the forests in Europe has been abandoned since the second
part of the 20th century, and natural succession is now proceeding. Furthermore, global change is altering site conditions, and with it forest productivity and species composition (cf. Bugmann 1997, Jarvis 1998, Shugart 1998, cf. IPCC 2001). As a consequence, the future growth and stand dynamics of these forests are likely to differ from past trajectories (Spiecker 1999). Investigating the changes in structure and species composition of these forests is a scientific challenge because the initial state is often unknown and the successional pathways are complex. The present paper addresses these issues, using the competitive dynamics of Scots pine (Pinus sylvestris L.) and pubescent oak (Quercus pubescens Willd.) in the formerly heavily exploited forests of Valais, an inner-Alpine dry valley in Switzerland, as a model. These forests are currently characterized by high pine mortality and the expansion of oak, which seems to be related to land-use change and increasing drought due to climate change (Rebetez & Dobbertin 2004, Weber 2005).

Forest development is most promisingly studied by following the fate of individual trees (Harper 1977). Tree rings provide a tool to retrospectively trace the growth of individual trees. They contain information not only on the climatic growing conditions, but also on the competitive level of a tree (Cook 1990). Competitive interactions between individual trees are usually reflected in periods of growth suppression and release (Banks 1991). In the last two decades, dendroecologists have often used release identification methods to reconstruct disturbance events and stand dynamics in forests (e.g. Lorimer 1980, Payette et al. 1990, Freligh & Reich 1995, Abrams et al. 1998, Bergeron 2000, Motta et al. 2002, Black & Abrams 2003, Bebber et al. 2004, e.g. Gutierrez et al. 2004, Rubino & McCarthy 2004). These analyses have proven useful in detecting the magnitude and frequency of disturbances (Black & Abrams 2003) and the general patterns of the species-specific responses during succession at the stand level. They seem, however, to be less appropriate for evaluating the intra- and interspecific competitive ability of individual trees, which can vary considerably over time. Moreover, focusing on successional trajectories over time, these analyses have hardly ever considered spatial relationships among single trees. Such spatial relationships have, however, been found to strongly affect the stem growth of individual trees (Biondi et al. 1994, Parish et al. 1999), and could therefore help to explain the growth patterns of uneven-aged and uneven-structured stands, such as those of abandoned forests.

In contrast, spatial interactions among individual trees have normally been investigated using static competition indices, which are lacking a temporal component. There is a long tradition
of such distance-dependent analyses of competition, in which the current growth of a target tree is analysed as a function of the sizes and distances of neighboring competitor trees (e.g. Hegyi 1974, Daniels 1976, Tome & Burkhart 1989, Biging & Dobbertin 1992, Stoll et al. 1994, Vacek & Leps 1996). These studies have shown a close relationship between competition indices and tree growth. However, these classic competition indices are static, and thus the dynamics of the system cannot be represented (Burton 1993).

To evaluate forest development, we propose and apply a method to analyse stand structures in terms of recent changes in the competition regime among single trees. We present a new approach to retrospectively trace the competitive dynamics of individual trees. Our “retrospective dynamic competition index” combines a temporal and a spatial component by comparing growth rates of a subject tree with the growth rates of its neighbors. The specific objectives of our study are (1) to cluster individual oak and pine trees of five whole stand plots according to different patterns of competitive dynamics and to analyse how these patterns are related to static competition indices and other growth parameters; (2) to examine competition and stand structure patterns for reconstructing stand dynamics as a basis for estimating future forest development; and (3) to specifically analyse drought as a factor influencing the competitive ability of pine compared to oak.

**Materials and Methods**

**Study area**

The study was carried out in Valais, an inner-Alpine dry valley situated in the south-western part of Switzerland (Fig. 1). The east-west oriented valley is characterized by a subcontinental-dry climate with high insolation. Precipitation is fairly low (between Visp and Sion less than 600 mm per year) because of the rain shadow exerted by the high mountain ranges in the South, Southwest and the North of the valley. Valais is known as the driest region in Switzerland and as one of the driest inner-Alpine valleys (Braun-Blanquet 1961, Ozenda 1985).
Fig. 1. Geographic position of the study area in Valais. The climate stations of Visp and Sion are indicated by grey triangles, and the study sites at Eschwald, Eggerberg and Salgesch by black dots.

In Valais, human impacts on past stand dynamics have been manifold. In the 19th century, large parts of the forests were devastated by foreign armies and by local communities to extract export timber, firewood and railway timber (Meyer 1950, 1951, 1952, Kempf & Scherrer 1982). For hundreds of years, goat grazing (Stuber & Bürgi 2001) and litter clearance (Stuber & Bürgi 2002) were widespread land-use practices that resulted in fairly open forest stands and in the suppression of the preferentially browsed (P. Mayer, unpublished data) oak trees. The regeneration of oak was additionally hampered because the acorns were removed by litter collecting. In contrast, the clear-cuttings of the 19th century and the use of wooded pastures facilitated the establishment of the light-demanding pioneer species pine.

However, after a few decades of abandonment, a change in the species composition of these forests is becoming apparent. While oak is spreading (1983-1993: +30% in stem number), pine locally shows high mortality rates (1983-1993: -6% in stem number) (WSL 2001). At present, pine and oak form extensive mixed stands in Valais’s low-elevation forests (below 1200 m a.s.l.).

Besides land-use change, changes in climate, i.e. a higher number of hot days (Rebetez & Dobbertin 2004) and different seasonality in moisture availability (Weber 2005) are thought to play a role in the competitive dynamics between pine and oak. Oak may benefit from its ability to adapt to drier conditions, whereas pine appears to suffer from prolonged summer

**Study plots**

In the lower montane pine forest belt of Valais, five whole-stand sampling plots were studied. They were selected so as to contain a random variety of tree growth in these forests. The study sites were situated between 710 and 1075 m a.s.l., where the vegetation is a mixture of dominating pine (*Ononido-Pinetum, Odontito-Pinetum* and *Erceto-Pinetum* (Braun-Blanquet 1961, Plumettaz Clot 1988)) and an increasing fraction of oak forest associations (*Saponaria-Quercetum pubescentis* (Burnand 1976)). The plots were chosen in those areas that showed a comparatively high oak proportion and potentially seemed to be most affected by changes in climate and land use (i.e. xeric site conditions, evidence of past forest management). Only by evaluating such later successional stages of mixed pine and oak stands, was it possible to estimate the ingrowth capability of pubescent oak in formerly pine-dominated forests. In compliance with these conditions, we chose two mixed pine and oak plots at Eschwald (46°15'35" N, 7°52'40" E), one plot at Eggerberg (46°18'50" N, 7°54'20" E) and two plots at Salgesch (46°19'25" N, 7°33'40" E) (Fig. 1).

The Eschwald and Eggerberg plots are located in the Visp sub-region, where the annual rainfall amounts to 599 mm at the SMI (Swiss Meteorological Institute) climate station of Visp for the period 1961-1990. The Salgesch plots belong to the Sion sub-region, with an annual rainfall of 598 mm at the nearby SMI climate station of Sion. However, between Visp and Sion, the precipitation sum from June to August increases from 123 mm to 162 mm, indicating less continental conditions in the Sion sub-region.

**Field sampling and processing of tree-ring data**

On each of the five sampling plots, which were 12 m radius, all the oak and pine trees with a minimum diameter at breast height (*dbh*) of 5 cm and a minimum height of 3 m were cored using an increment borer. Two cores were taken at breast height to analyse growth and to derive competitive dynamics, and one core was extracted at the base of each tree to determine its age. Damaged trees, tree stumps and dead trees were cored if possible and marked as such.
For each tree, the x- and y-coordinates, height \((h)\), \(dbh\), social class \((soc:\ 1=\text{dominant}, \ 2=\text{codominant}, \ 3=\text{subdominant}, \ 4=\text{suppressed} \ (\text{cf. Kraft 1884})\)), and height proportion of crown to stem \((cpr:\ 1=\text{low proportion}, \ 4=\text{high proportion})\) were recorded. Additionally, for pine trees, the height proportions of stem with dead branches to total stem height \((dbr:\ \text{from 1=low proportion to 9=high proportion})\) were estimated as a measure for light competition (Makinen & Colin 1999).

Tree rings were measured on a Lintab3 measuring system (F. Rinn S.A., Heidelberg, Germany) with a resolution of 0.01 mm. The TSAP tree-ring software (Rinn 1996) was used to crossdate the cores (Fritts 1976, Schweingruber 1988). Tree-ring data from all the trees sampled could be successfully used for the further analyses, although measuring and crossdating the sometimes strongly suppressed trees at these rather extreme sites was fairly difficult. The ring widths of the two cores of each tree were averaged and converted to basal area increment \((bai)\) since \(bai\) is mathematically less biased by stem geometry, which makes it less dependent on tree age. \(bai\) is also a better estimate for the effective resource exploitation of a tree.

**Analysis of competitive dynamics**

Using \(bai\) data, we derived a retrospective dynamic competition index to analyse the competitive ability of individual oak and pine trees over time. This calculation was based on the assumption that high \(bai\) growth values imply a high competitive ability (Bazzaz 1996, Begon et al. 1996), but also a smaller risk of mortality (McClenahen 1995, Bigler & Bugmann 2004). Trees from the same stand usually show a common signal in their tree-ring series (Fritts 1976), which is related to climate and therefore has been the focus of many dendroclimatological analyses. In our investigations, however, we were not interested in extracting this common signal, but in explaining the differences in the individual growth patterns. Thus, we calculated \(bai\) ratios of neighboring trees over time, which resulted in the partial removal of the common climate signal.

To avoid edge effects, the analysis was performed for all the trees in an inner circle 9.5 m in radius, with a circular neighborhood zone 2.5 m in radius around each single investigated tree. This relatively small size of the neighborhood zone was justified by the comparably low maximum tree height and the fairly open forest stands. Within this neighborhood zone,
competition was expected to be distance-dependent, i.e. to decrease linearly with increasing distance from the investigated subject tree. Based on the above requirements, we calculated the retrospective dynamic competition index as follows:

\[ C_{i,t} = \sum_{j=1}^{n} \frac{bai_{j,t} / bai_{i,t}}{dist_{j,t}} \]

where \( C_{i,t} \) is the competition load for the subject tree \( i \) in the year \( t \), \( bai_{j,t} \) is the basal area increment of the competitor tree \( j \) in the year \( t \), and \( bai_{i,t} \) is the basal area increment of the subject tree \( i \) in the year \( t \), \( dist_{j,t} \) is the distance between the subject tree \( i \) and the competitor tree \( j \), and \( n \) is the number of competitors in the neighborhood zone. If a subject tree has zero competitors, the index takes a value of 0. In all other cases, the index becomes higher the more competitors a subject tree has, and the better these competitors grow in comparison to the subject tree. When tracing the development of the competition index over time, we speak of the “competitive dynamics” of a tree, which is characterized by the level of competition the tree faces, i.e. the value of \( C_{i,t} \), and the trend in competition over time. Both level and trend in competitive dynamics were explored by plotting annual cumulative curves of the competition index over time.

The level of dynamic competition did not differ significantly between the two species when comparing intraspecific (oak with oak, pine with pine neighbors) with interspecific competition indices (oak with pine, pine with oak neighbors). The influence of a competitor oak or pine tree was therefore assumed to be equal. The analysis was done for the time span 1960-2001, since most trees were older than 40 years and the period was long enough to detect changes in competitive relationships but short enough to find evidence of management activities (stumps) and mortality (dead trees) on each plot.

**Clustering trees with similar competitive dynamics**

All the competition curves of the single trees from the five plots were analysed in combination. To reveal different patterns of competitive dynamics within the sampled oak or pine trees, we performed a cluster analysis. Starting from annual cumulative curves of the competition index of all the subject pine or oak trees over time, we applied the average linkage method using the statistics software R, version 1.6.2 (R Development Core Team
2003) for clustering. Based on the resulting dendrograms, groups of trees with similar competitive dynamics were defined. For each of the resulting groups, we calculated an average cumulative competition curve.

For comparison with the retrospective dynamic index, two static competition indices and three additional growth parameters were calculated for the sampling year 2002. The classic distance-dependent competition index that was introduced by Hegyi (1974) was calculated as follows:

\[
CI_{hi} = \sum_{j=1}^{n} \frac{dbh_j/dbh_i}{dist_{ji}}
\]

where \( CI_{hi} \) is the competition index for the subject tree \( i \), \( dbh \) is the diameter at breast height, \( dist_{ji} \) is the distance between the subject tree \( i \) and the competitor tree \( j \), and \( n \) is the number of competitors in the neighborhood zone.

Furthermore, we introduced a competition index that focuses on tree height compared to the competitors’ height. This index was calculated as follows:

\[
CI_{2i} = \left( \sum_{j=1}^{n} H_j \right) / n; \text{ if } (h_i > h_j) \Rightarrow H_j = 1; \text{ else } \Rightarrow H_j = 0
\]

where \( CI_{2i} \) is the competition index for the subject tree \( i \), \( h_i \) is the height of the subject tree \( i \), \( h_j \) is the height of the competitor tree \( j \), and \( n \) is the number of competitors in the neighborhood zone. The resulting index is 1 if the tree is taller than all its competitors; it is 0 if the tree is smaller than all its competitors and ranges between 0 and 1 in the other cases.

The additional three parameters are based on growth rates and were chosen as supplementary measures for the competitive ability of a subject tree. Sapwood area (sap) is known to be related to leaf area (Grier & Waring 1974) and was calculated by summing up the basal area increment of the sapwood rings. \( Bai0 \) was calculated as the sum of the basal area increment over the last ten years. Finally, \( relbai \), the ratio between \( Bai0 \) and total basal area of the subject tree, was added as a relative measure of its growth capacity. The resulting values were also averaged according to the clusters of the dynamic indices for comparison.
Competitive dynamics and drought

The patterns of the competitive dynamics of the pines were compared to those of the oaks by calculating the interval trends (Schweingruber 1988, 1990) with the individual trees’ retrospective dynamic competition curves. For the interval trend, the number of ascending and the number of falling curves for each year-to-year interval was recorded. The percentage of ascending intervals within the dynamic competition curves of the pines was subtracted from the percentage of ascending intervals within the curves of the oaks. In the resulting curve, values above 0 mean a competitive advantage for the pines, whereas values below 0 mean a competitive advantage for the oaks. This difference curve of competition was evaluated against the moisture index Ppot (Weber 2005) across time to reveal whether drought as a limiting factor influences the competitive dynamics of oak and pine. Ppot was calculated as the difference between precipitation and potential evapotranspiration according to Thornthwaite (1948). For the two sub-regions Visp (Eschwald and Eggerberg) and Sion (Salgesch), separate moisture indices and separate interval trends of competitive dynamics were computed. The interval trends were analysed between 1970 and 2001 because the number of trees used for the analysis (replication) was fairly constant during that period.

Results

The age and dbh structure of all the trees on the 5 sampling plots indicated a change in species composition towards oak (Fig. 2), as pine was more frequent in the upper dbh and age classes, whereas oak was noticeably more abundant in the lower dbh and age classes. (Note that the lowest age class (20-40 years) does not constitute a representative sample because trees with a dbh smaller than 5 cm and a height smaller than 3 m were not included.)

A total of 456 trees were cored, measured and cross-dated. The sample sizes, the numbers of dead trees and stumps, and the total number of trees taller than 3 m are listed for each plot separately in Table 1. Overall, 19 pine stumps and two dead pine trees were recorded that could not be cored due to advanced wood decay (Table1). As wood decay is quite slow in such dry climates, we can assume that these trees died before the period of analysis. Additionally, three oak stumps could not be sampled, of which two were not neighbors of trees analysed in the competition analyses.
Table 1. Number of trees sampled (top) and selected stand structure parameters (bottom) for the five plots in Valais. For the stand structure parameters, stem numbers and basal areas were extrapolated from the plot area (452.4 m²) to one hectare.

<table>
<thead>
<tr>
<th>Number of samples</th>
<th>Eschwald lower</th>
<th>Eschwald upper</th>
<th>Eggerberg</th>
<th>Salgesch lower</th>
<th>Salgesch upper</th>
<th>total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Living oaks</td>
<td>30</td>
<td>36</td>
<td>50</td>
<td>110</td>
<td>74</td>
<td>300</td>
</tr>
<tr>
<td>Living pines</td>
<td>14</td>
<td>56</td>
<td>12</td>
<td>22</td>
<td>22</td>
<td>126</td>
</tr>
<tr>
<td>Stumps: total / not sampled</td>
<td>13 / 3</td>
<td>16 / 11</td>
<td>2 / 2</td>
<td>4 / 4</td>
<td>2 / 2</td>
<td>37 / 22</td>
</tr>
<tr>
<td>Dead pines: total / not sampled</td>
<td>2 / 0</td>
<td>10 / 2</td>
<td>1 / 0</td>
<td>1 / 0</td>
<td>3 / 0</td>
<td>17 / 2</td>
</tr>
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Fig. 2. Dbh (a) and age histograms (b) for all the trees on the five sampling plots. Only pine (no = 126) and oak (no = 300) trees with a dbh greater than 5 cm and a height above 3 m were considered.
In the inner circles 9.5 m in radius, 132 oak and 40 pine subject trees could be analysed for retrospective dynamic competition, reflecting the abundances of the two species in the forests studied. The individual trees’ cumulative dynamic competition curves were grouped according to similar patterns, for pine and oak separately. The clustering procedure divided the curves into well-defined clusters (Fig. 3).

![Cluster diagram](image)

Fig. 3. Clustering of the cumulative retrospective dynamic competition indices of pines and oaks by average linkage. The height axis was log-transformed. Four Clusters were segregated for both species (oak1-4, pine1-4).

For both species, a large percentage of the trees (87% of the oak, 70% of the pine trees) revealed very similar competitive dynamics, i.e. constant competition on a relatively low level (Fig. 4). These trees were considered as one group (oak1, pine1) and were not subdivided any
further to emphasize their difference from the other competitive patterns. One single oak tree was excluded from the further analysis steps because it made up a cluster of its own. In this way, four patterns of competitive dynamics were identified for both pine and oak, ranging from a low (oak1, pine1) to a high competitive level (oak4, pine4) (Fig. 4). For oak, the competitive patterns generally were consistent with the current values of the static competition indices and the other growth parameters (Fig. 4). As an exception, oak3 (3 trees) would be classified as being suppressed more strongly than oak4 (2 trees) based on dbh, height, social class and also the height-dependent index CI2. Except for the first ten years of oak4, the oaks showed nearly straight competition curves, i.e. no notable increase in competition during the investigated period. The dynamic competition index for oak3 and oak4 even flattened somewhat during the last 10 years, indicating a slight decrease in competition. Among the four competition levels in pine, pine2 (6 trees) and pine4 (2 trees) showed a pronounced increase of competition during the last 10 years. In fact, most current growth parameters (soc, cpr, dbr, sap, bai10, relbai) suggested that today, pine2 had a lower competitive ability than pine3. In particular, the proportion of dead branches as a measure for recent crown competition was higher in pine2, being nearly as high as in pine4. Unlike the dynamic indices, the static competition indices $CI_1$ and $CI_2$ concealed the increasing competitive pressure on the trees in pine2.

Fig. 4. The four competitive patterns of oak (grey) and pine (black) trees. Cluster averages of the cumulative retrospective dynamic competition indices (diagram left) are compared to the cluster averages of the static competition indices ($CI_1$ and $CI_2$) and the other growth parameters in the year 2002 (table right). Parameter descriptions: $No =$ number of trees in each cluster; $NoC =$ average number of competitors for subject trees belonging to a certain cluster; $CI_1$ and $CI_2 =$ competition indices; $h =$ tree height [m]; $soc =$ social class (1 dominant, 2 codominant, 3 subdominant, 4 suppressed); $cpr =$ crown proportion (lowest class 1, highest class 4); $dbr =$ dead branches along the stem (1 low proportion, 9 high proportion); $sap =$ sapwood area [cm$^2$]; $bai10 =$ basal area increment of the last 10 years [cm$^2$]; $relbai =$ ratio between bai10 and total basal area.
In comparison to basal area increment (bai), the competition index contained rather different information. If we had looked at bai alone (Fig. 5), the trees would not have been grouped into the same clusters as for competition, since the bais of trees within the clusters varied markedly. For example, both in the high-competition clusters oak4/pine4 and in the low-competition clusters oak1/pine1, some trees had very slow growth. Nevertheless, some general patterns in bai were visible. Trees in cluster pine1 grew well in the period 1965-1985, but growth decreased in many trees during the last 15 years. A similar pattern was found in pine2 and pine4. Only the trees of cluster pine3 grew better after 1975. In contrast, the average growth of all four oak clusters increased over time, most markedly after 1975. The oaks nevertheless displayed smaller average bais than the pines.

![Fig. 5. Basal area increment (bai) of all subject trees grouped according to the four competition clusters in oak and pine. Thick black line: average bai of each cluster. The dashed line marks the start of the period of dynamic competition analysis.](image-url)
Oaks tended to have a larger height at a certain dbh (Fig. 6) and to grow better at a given dbh (Fig. 6), although the differences were statistically not significant (test for homogeneity of slope (Sokal & Rohlf 1995)). In 2002, most of the oaks had a dbh smaller than 25 cm. In the future, these differences in the dbh-height relation between pine and oak may therefore gain significance. Contrary to our expectations, neither tree height nor basal area increment of the last ten years (bai10) were related to tree age.

![Fig. 6. Differences in the growth of oak and pine. Height and bai10 (basal area increment of the last ten years) show a relationship with dbh (left), but not with age (right). Significance of the linear model: * p < 0.05; ** p < 0.01; *** p < 0.001.](image)

Oaks and pines differed in their interval trends of ascending competition over time (Fig. 7). The difference curve of the interval trends partially ran parallel to the moisture index Ppot. The correlation between the two curves was fairly good for trees in the Visp sub-region (r=0.43), but it was lower for trees in the Sion sub-region (r=0.31). A competitive disadvantage of the pines often coincided with dry years (i.e. low Ppot), whereas a competitive disadvantage of the oaks was less frequent, and was often observed in or just after moist periods (i.e. high Ppot). Overall, the curves tended to be more similar in the second half of the investigated period. The interval trend did not show a clear trend in the competitive regime between pine and oak over the 30 year period.
Fig. 7. Difference curve of positive intervals in the competitive dynamics of oaks and pines (black) compared with the yearly moisture index Ppot (grey). Eschwald upper and lower plot and Eggerberg belong to the Visp sub-region (top), Salgesch upper and lower plot to the Sion sub-region (bottom). Values above 0 indicate low competitive ability of oaks, whereas values below 0 indicate low competitive ability of pines.

Discussion

Reconstruction of competitive dynamics

By using a retrospective dynamic competition index and clustering the trees according to the similarity of competitive patterns (Figs. 3 and 4), we were able to distinguish three major competitive patterns, which provide useful information on stand dynamics in addition to those obtained using static indices. First, a majority of the trees shows relatively constant competition over time (linear cumulative competition curves). Second, some trees can be found with recently increasing competition (cumulative curves deviate from linear course: pine2 and pine4). Third, some trees are growing under a high competition regime even though constant over time (curves with a comparably large slope: oak3 and oak4).

Unlike many studies on the stand structure of mixed forests, we found that height and basal area growth are not related to tree age for both pine and oak (Fig. 6). This result is indicative
of the highly variable tree growth in these stands, which on the one hand has been altered strongly by past land-use practices (Rigling et al. 2004), and on the other hand is constrained by the xeric site conditions (Rigling et al. 2002, Weber 2005). In these forests, we find various tree growth forms: Both young and old trees can be suppressed (i.e. small size and low growth rates) or become dominant (i.e. large size and high growth rates) (Fig. 6). Given this variability of growth forms, the new method needed for analyzing the competitive abilities of single trees over time.

With respect to both the static and the dynamic competition indices, oaks seem to be more constant in their competitive ability in the long term, whereas some pines show inconsistent competitive patterns (Fig. 4). As a consequence, further growth declines of some pine trees can be expected, thus emphasizing the change in species composition that is evident from the basic stand structure analyses (Figs. 2 and 6).

**Competition as a factor for forest succession in Valais**

Estimating future forest succession is important for forest management. This is also true for the low-elevation forests in Valais, which often protect against natural hazards and form a characteristic landscape, harboring one of the Swiss biodiversity hotspots (Wohlgemuth 1998). Therefore, it is relevant to understand how differences in the competitive ability between oak and pine trees may alter stand dynamics, and at the same time species composition.

A change in species composition towards a higher oak proportion is evident from the analyses of stand structure and both the dynamic and static competition indices. The reasons for the observed change are manifold and complex (Rigling et al. 2004, Weber 2005). However, the major drivers underlying the currently observed successional processes are changes in land use. Historical land-use activities, which mainly favored the pioneer species pine, have decreased strongly over the 20th century, and these forests are now developing towards a later successional state, where pine as a light demanding species is particularly subject to increasing intra- and interspecific competition for light. The patterns of both the competitive dynamics (Fig. 4) and the bai growth of pine (Fig. 5) illustrate that some pines have already entered the phase of increasing light competition and very slow growth, which may finally lead to higher mortality (Bigler et al. in press). This case study of Valais thus illustrates how a
changed disturbance regime results in altered successional patterns and stand structures (Linder et al. 1997).

Parallel to land-use changes, climatic changes also affect the growth and survival of these two tree species in Valais (Rebetez & Dobbertin 2004, Weber 2005). Based on the interval trend analysis (Fig. 7), pines appear to be subject to higher competition in dry years, whereas oaks face higher competition in moderate years. These opposing growth patterns can be explained by the different life history strategies of the coniferous, sub-boreal pine vs. the deciduous, sub-Mediterranean oak (Weber 2005). Because of their perennial needles, pines react less flexibly to drought than oaks, which have short-lived leaves. Moreover, pines presumably develop a shallower rooting system than oaks, which makes them more susceptible to drought (Waring 1987). Also, the growth response of oak was found to indicate a better adaptive capacity to a changing climate (Weber 2005), which, in Valais, has been characterized by warmer conditions particularly since the 1980s (Rebetez & Dobbertin 2004) and by a shift in the seasonality of moisture availability (Weber 2005).

In fact, in the climatically more extreme Visp sub-region, the difference curve of ascending intervals in the competitive dynamics of oaks and pines correlated more strongly with drought than in the more oceanic Sion sub-region (Fig. 7), thus supporting the view that the species-specific drought response plays an important role in modulating interspecific competition between oak and pine. In a future changing climate, the diverging effect of the species-specific drought response is likely to gain further importance.

**Deriving competitive dynamics from tree-ring data**

Static competition indices provide a powerful tool to analyse the competitive structure of a forest stand. These competition indices do, however, have considerable limitations (Burton 1993). The retrospective dynamic competition index proposed in our study has some distinct advantages. First, besides the spatial component, it also contains a temporal component, and thus allows us to reconstruct competitive dynamics over time. Second, by looking at both the level and the trend in competitive dynamics, we were able to identify 1) trees with increasing competition, even though they are growing at a low competition level (groups pine2 and pine4), and 2) trees with constant competition, even though they are growing on a high
competition level (groups oak3 and oak4 in Fig. 4). The latter demonstrates that competition can be “intense without being significant” (Burton 1993).

Some problems inherent to the exploration of inter-tree competition remain, nevertheless, unsolved. Belowground effects on competitive dynamics are difficult to study and therefore scarcely understood. Disentangling aboveground (light) and belowground (water and nutrients) competition is only feasible in field studies under experimental conditions where the influencing factors can be separated from each other. Generating such conditions could be difficult in Valais because of the strong past anthropogenic disturbances that have led to the heterogeneous growth forms of the trees and probably have overridden all other influencing factors.

In our study, the bai values of pine and oak were assumed to have an equal effect on the bai growth of neighboring trees, although morphology varies considerably between the two species. However, this approach was justifiable and even appropriate because the comparison of intraspecific (oak with oak competitors, pine with pine competitors) versus interspecific (oak with pine competitors, pine with oak competitors) static and dynamic indices failed to reveal any interspecific differences. Consequently, it appears that pine is outcompeted equally well by both its pine and oak neighbors. Unfortunately, we did not record leaf area or crown volume variables, which would have enabled us to directly calibrate the competitive effect of pine vs. that of oak. Specifying the species-specific influence is a well-known problem in multi-species studies (Biondi et al. 1992, Berger & Hildenbrandt 2000, Uriarte et al. 2004).

In spite of these limitations, using the new dynamic competition indices allowed us to directly compare the competitive ability of young and old trees over the same time span, which is a considerable advantage over classic age-stratified growth analyses (e.g. Motta & Nola 2001). For stratification, the statistical clustering of the cumulative retrospective dynamic indices offers an alternative in those cases where age-stratified growth analyses are not feasible, i.e. within uneven-aged and uneven-structured forest stands. With our statistically-based approach, however, we were still able to reveal the major competitive patterns over time.

Moreover, the retrospective dynamic competition index developed here integrates more information than ring-width curves alone. This can be seen by comparing the groups of competitive dynamics obtained from the cluster analysis (Fig. 4) with the individual bai
curves that were grouped according to the same clusters (Fig. 5). While the tree-ring series account for temporal variability only, dynamic competition indices combine a temporal and spatial element, so that the growth potential of the neighborhood becomes relevant for predicting the competitive ability of a tree.

Conclusions

The new retrospective dynamic competition index proposed here allows us to detect the trend underlying current competition, whereas classic static competition indices can describe only the current level of competition. The application of the retrospective dynamic competition index is particularly suitable in the case of 1) uneven-aged and uneven-structured stands where age-stratification fails, 2) stands with heterogeneous tree growth forms due to other factors, e.g. mixtures of light-demanding and shade-tolerant species, and 3) stands with heterogeneous spatial patterns. Combining the new dynamic index with standard static indices seems promising as a way of analyzing past and estimating future stand development. The bai-based dynamic index provides a method to trace competitive dynamics with a high temporal resolution without repeated assessments, which represents a major advance in forest dynamics analyses. The dynamic index allows us to identify whether and when outcompeting processes are likely to occur, which can help in disentangling effects of land-use and climate change.

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Retrospective dynamic competition indices


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Chapter III

Investigating the impact of grazing on the dynamics of mixed Pinus sylvestris and Quercus pubescens stands by applying a forest gap model

Submitted as:
Pascale Weber¹, Andreas Rigling¹, Harald Bugmann². Investigating the impact of grazing on the dynamics of mixed Pinus sylvestris and Quercus pubescens stands by applying a forest gap model. Ecological Modelling.

¹Swiss Federal Institute for Forest, Snow and Landscape Research, WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland
²Forest Ecology, Department of Environmental Sciences, Swiss Federal Institute of Technology (ETH), ETH Zentrum, CH-8092 Zürich, Switzerland

Abstract

Only recently, studies of forest succession have started to include the effects of browsing by wild or domestic ungulates. We aim to contribute to this topic by analysing the influence of grazing on the long-term coexistence of Scots pine (Pinus sylvestris L.) and pubescent oak (Quercus pubescens Willd.) in the low-elevation forests of an inner-Alpine dry valley. The forest gap model ForClim was first adapted to these site conditions by examining the site-dependent sensitivity of the model with regard to the species-specific parameterisation of the drought tolerance as well as the light demand of establishing and adult trees. In a second step, the behaviour of the model was investigated with respect to different grazing intensities and species-specific browsing susceptibilities. The last step was the application of a grazing scenario based on forest history, with 150 years of heavy browsing at the beginning of the simulated forest succession, followed by less intensive grazing pressure.

By comparing empirical with simulated data, it was evident that the model underestimated Scots pine basal area if succession was simulated without grazing. Introducing grazing led to a more realistic, stronger representation of Scots pine in the model. Regeneration of the more
browsing-susceptible pubescent oak was seriously suppressed during the simulated intense grazing period, which led to a higher occurrence of Scots pine in the model. Although after 400 years of simulated succession pubescent oak reached nearly the same basal area as without intense grazing, succession was strongly delayed. The model application suggests that goat grazing allows for a much longer period of codominance of Scots pine and pubescent oak in these forests. The changes in the simulated successional pathways support the view expressed in other studies that human impacts may have strong effects on forest succession. Our results allow for a first qualitative estimate, and they make clear that the representation of browsing in forest succession models needs to be improved further.

**Keywords:** browsing; drought; ecological modelling; forest succession; human impacts; land-use change

### Introduction

Forest gap models have been used widely to examine forest succession as a complement to field observations and experiments (Botkin et al. 1972, Shugart 1984, Bugmann 1996). However, being adapted to a relatively broad spectrum of environmental conditions, these models are most appropriate for simulating forest succession under general temperate and boreal conditions, for which they have originally been developed. Because of their rather general nature, they have less often been used for site-specific investigations, which typically would require specific information for achieving local precision (Levins 1966). Among these special cases that demand more specific and local knowledge are forests under xeric site conditions or sites with strong human impacts, e.g. forest grazing.

To date, most simulation studies with these models have explicitly excluded human interventions (e.g. Solomon 1986, Kienast & Kuhn 1989, Bugmann 1996), and only recently some efforts have been undertaken to evaluate how browsing by domestic and wild ungulates may influence future forest development (Jorritsma et al. 1999, Kienast et al. 1999, Seagle & Liang 2001, Risch et al. 2005). For example, Kienast et al. (1999) simulated high-elevation forests under changing herbivore pressure and found that, although changes in successional pathways were not dramatic, forest structure was considerably changed. In a field study by
Ares et al. (2003), grazing was indeed suggested to be responsible for changes in forest structure in general and the height-diameter relationship of trees in particular.

Intensive browsing may cause altered rates of succession as a result of species-specific life history characteristics (Seagle & Liang 2001). Differences in the browsing susceptibilities of early and late successional species may thus lead to an accelerated or delayed succession. This does not imply that final forest composition will necessarily be affected (Seagle & Liang 2001). However, Blatt et al. (2001) presented a model for insect herbivory where they showed that herbivory may also ensure a stable coexistence between early and late successional tree species by effectively preventing succession. From a theoretical point of view, we may explain such coexistence patterns by the intermediate disturbance hypothesis (Connell 1978), where dominance reduction (Wohlgemuth et al. 2002) may lead to higher (tree) species diversity.

In the present study, we focus on the influence of historical forest grazing in combination with rather extreme site conditions close to the dry treeline in the European Alps. Simulating forest succession for such sites appears to be more difficult than for mesic sites, as it requires a precise knowledge of the ecologically important processes at the specific location (cf. Bugmann & Solomon 2000). For low-elevation forests in Valais, an inner-Alpine dry valley in Switzerland, two forest models, FORECE (Kienast & Kuhn 1989) and ForClim (Bugmann 1996), and different versions of the latter model (ForClim 2.6, cf. Bugmann & Cramer 1998) resulted in two completely different forest types, one dominated strongly by Scots pine (*Pinus sylvestris* L.), the other mostly dominated by oak species (*Quercus* spp.). These differences were caused by slight differences in the parameterisation of the drought tolerance of oak and pine and by adaptations in the soil water balance model. These differences in model behaviour demonstrate that models may exhibit a high sensitivity to such changes when applied under extreme site conditions.

Up to now, anthropogenic impacts on forest succession have not been included when applying succession models for Valais, although it is most likely that current forest structure and composition are influenced strongly by historical land-use practices. In the last decades, a change in species composition in these forests has become apparent. While Scots pine is declining in many areas, pubescent oak is spreading (Kienast et al. 2004, Rigling et al. 2004, Weber et al. 2005a). However, whether both species will coexist in these low-elevation
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Forests in the future is an open question and currently under investigation (Rigling et al. in press). For estimating future stand development, a better understanding of the influences of past anthropogenic disturbances on current forest composition is needed. With the approach presented here, we aim to contribute to answering this question.

Specifically, we aim to contribute to a better understanding of the impact of forest grazing on succession and species coexistence in forest ecosystems, using the mixed Scots pine-pubescent oak forests of Valais as a case study. The modelling approach should help to elucidate how current forest composition and structure in Valais have evolved, and whether succession was possibly delayed (or accelerated) because of historical grazing practices. The specific objectives of our study are 1) to improve the parameterisation of Scots pine and pubescent oak in the model, 2) to simulate the succession of forests close to the dry treeline and 3) to evaluate the influence of a forest history-based grazing scenario on model behaviour by comparison with measured data from five forest stands.

Material and Methods

Field data

The study sites in the inner-Alpine valley Valais are characterised by a subcontinental dry climate with high insolation. The SMI (Swiss Meteorological Institute) climate station in the valley bottom at Sion (482 m a.s.l.) recorded a mean annual temperature of 9.2°C and an annual precipitation sum of 598 mm between 1961 and 1990. The sampled forest stands are located on steep valley slopes at elevations between 590 and 1075 m a.s.l. The prevailing soil types were classified as Regosols, Rendzic Leptosols and Distric Cambisols with low available water capacities between 56 and 166 mm (Weber et al. 2005a).

In the field part of the study, eight mixed pubescent oak and Scots pine plots of 12 m in radius (equivalent to an area of 452.4 m²) were sampled in 2002. All trees taller than 3 m were recorded and their diameters at breast height (dbh) and tree heights were measured. Tree age was estimated from increment cores extracted at the stem base. For each plot, basal area of pubescent oak and Scots pine was calculated from the dbh data of the single trees.
Model study

Stem numbers and basal areas of both species recorded on the investigated plots were compared with stem numbers and basal areas simulated by the forest gap model ForClim (Bugmann 1996). The version used here is ForClim V2.9.3, which includes a new water balance submodel (Bugmann & Cramer 1998), modified climatic response functions (Bugmann & Solomon 2000) and an improved growth function (Risch et al. 2005). In gap models, establishment, growth and mortality of individual trees are simulated on small patches of land (often 1/12 ha) as a function of species natural histories and the extrinsic and intrinsic conditions of the stand. The major state variables are the diameters of individual trees, from which a number of output variables such as biomass and basal area can be calculated.

ForClim consists of three modular submodels: ForClim-E is a submodel for the abiotic environment, ForClim-S is a submodel for soil carbon and nitrogen turnover, modified from Pastor and Post (1985), and ForClim-P is a submodel for tree population dynamics based on the well-established concept of gap dynamics (Watt 1947, Shugart 1984).

Tree establishment rates are determined from light availability at the forest floor, browsing intensity, and absolute winter minimum temperature. These three factors are formulated as species-specific environmental filters (“flags”): light availability and winter temperature are used as thresholds that prevent regeneration when it is too dark or too cold for a species, whereas increasing browsing intensity acts to reduce the species-specific establishment probability in a continuous manner. Additionally, in ForClim V2.9.3 the number of saplings to be established in the recruitment routine is tied to the shade tolerance of adult trees (parameter $kLa$): the larger $kLa$ and thus the stronger the pioneer character of a species, the more saplings are being established, reflecting an ecological trade-off (Risch et al. 2005).

Actual growth of each tree is simulated by calculating a maximum diameter-specific growth rate that is decreased by four growth-limiting factors: light availability, degree-day sum, soil moisture and nutrient availability. Species-specific parameters that had been estimated from the general autecological literature (cf. Bugmann 1994) are used in the formulation of these growth factors. For example, the light growth factor is a function of the shade tolerance of a given tree species ($kLa$) and the light availability across the canopy ($gAL$), which is calculated
using the Beer-Lambert law (Botkin et al. 1972) (Fig. 1a). The soil moisture growth factor is depending on the species-specific maximum drought tolerance ($k_{DrT}$) and the drought index ($u_{DrStr}$), expressed as the annual evapotranspiration deficit (Fig. 1b).

![Diagram](image1.png)

Fig. 1. Two of the four growth-limiting factors: a) Light growth factor $g_{ALGF}$: $g_{AL} = $ light availability in % of full sunlight, $k_{La} = $ shade tolerance of adult trees ($1 = $ high, $9 = $ low). b) Soil moisture growth factor $g_{SMGF}$: $u_{DrStr} = $ drought index ($0 = $ moist, $1 = $ very dry), $k_{DrT} = $ drought tolerance of adult trees.

Tree mortality is modelled as a combination of an age-related and a stress-induced mortality rate (Botkin et al. 1972, Kienast 1987), giving rise to high mortality of small trees due to strong competition for light, and a high mortality of old trees due to low vigour (cf. Bugmann 1994).

In this study, the species-specific parameterisation of Scots pine and pubescent oak in the model was re-evaluated and the sensitivity of the model regarding different parameter sets was analysed for the low-elevation site conditions of Valais. In a second step, the influence of grazing on stand development was evaluated by applying a grazing scenario.

**Parameterisation of Scots pine and pubescent oak**

The parameters for Scots pine and pubescent oak were estimated and adjusted based on recently gathered data regarding the ecological properties of both species in Valais (Weber et al. 2005a, Weber et al. 2005b, Rigling et al. in press). The parameterisation of Scots pine was usually not changed, since the autecology of this widely distributed species is known rather well. In contrast, pubescent oak was originally parameterised in a similar manner as other native oak species in Switzerland (*Quercus petraea* and *Q. robur*), because of insufficient
knowledge of the ecology of this economically uninteresting species. From our better understanding of pubescent oak in Valais, it was clear that some parameter values had to be changed considerably.

Concerning tree establishment, we changed the parameterisation for the browsing susceptibility ($kBrow$) and the light requirement of tree saplings ($kLy$). Concerning tree growth, we adapted the parameterisation for the drought tolerance ($kDrT$) and the shade tolerance of adult trees ($kLa$). All four parameters were estimated anew for pubescent oak, whereas for Scots pine only $kLy$ was modified. Additionally, we changed the parameter values for the initial height-diameter growth rate of a tree ($kS$), for maximum tree height ($kHMax$) and for maximum age ($kAMax$). These parameter values and the basis for their adjustment are described in detail below.

**Establishment:**

Browsing susceptibility ($kBrow$) was estimated anew based on the results of a field study in Valais (Rigling et al. in press). The value of the parameter $kBrow$ represents the annual browsing incidence as a fraction of the sapling population under standard grazing conditions ($uBrPr = 1$). In the original parameterisation, $kBrow$ of Scots pine was very low (0.01), whereas $kBrow$ of pubescent oak was somewhat higher (0.06). In Valais, more than 20% of oak, but less than 5% of pine saplings were found to be heavily browsed (Rigling et al. in press). Considering the low proportion of browsed Scots pine saplings in Valais, the value for Scots pine was not changed, but $kBrow$ of pubescent oak was increased to 0.1 because of the relatively high proportion of browsed saplings found. Sapling mortality and browsing pressure have limited comparability; in the model, it is assumed that for $kBrow = 0.1$, sapling mortality is 20% if browsing pressure is increased to $uBrPr = 2$ (cf. Fig. 2). This new parameterisation seems realistic, taking into account that some browsed saplings will finally survive, and considering the difficulty of estimating browsing percentages in the field (Senn & Suter 2003).
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Fig. 2. The probability that establishment is prevented ($g_{BrP}$) depends on browsing pressure ($u_{BrPr}$) and the browsing susceptibility of the tree species ($k_{Brow}$) in ForClim V2.9.3.

Pubescent oak has often been assumed to be similarly light demanding as other native oak species in Switzerland (Quercus petraea, Quercus robur) because not many data on the ecology of pubescent oak were available. In the original parameterisation, pubescent oak was therefore equally light demanding ($k_{Ly} = 0.3$) as Scots pine ($k_{Ly} = 0.3$), with typical values for the $k_{Ly}$ parameter of European tree species ranging between 0.025 and 0.4, being defined as the fraction of full sunlight. In contrast, Rigling et al. (in press) found that pubescent oak saplings were frequent also under closed canopies, whereas Scots pine saplings occurred frequently only under open canopies. The light requirement parameter $k_{Ly}$ was therefore decreased in oak (from 0.3 to 0.1) and increased in pine (from 0.3 to 0.4).

Growth:

In the model, the light growth factor $g_{ALGF}$ is a function of the shade tolerance parameter $k_{La}$ of a tree species (cf. Fig. 1a). Scots pine is assigned the highest value ($k_{La} = 9$), i.e. adult trees of this species are assumed to have a very low shade tolerance. Pubescent oak, again, has originally been assigned the same value as sessile oak (Quercus petraea) ($k_{La} = 7$). Analyses of the competition between Scots pine and pubescent oak in Valais showed that pubescent oak trees are able to grow at a constant level, even under a relatively high level of competition (Weber et al. 2005a). Taking this into account, the light requirement parameter for pubescent oak adult trees ($k_{La}$) was decreased to 6, which is the same value as for Corylus avellana and Fraxinus excelsior.
Drought tolerance was hypothesised to be a key parameter for the competition between the sub-Mediterranean pubescent oak and the sub-boreal Scots pine (Weber et al. 2005b). The drought tolerance parameter \( k_{DrT} \) specifies the evapotranspiration deficit during the growing season at which tree growth comes to a halt (0 = no deficit, 1 = very high deficit, cf. Fig. 1b). In the original parameterisation, Scots pine was among the three most drought-tolerant European tree species (0.37), whereas pubescent oak was supposed to be less drought-tolerant (0.33). The drought tolerance parameter \( k_{DrT} \) was re-estimated based on recent studies on the differences in drought tolerance between the two species, which indicated that pubescent oak is better adapted to drought than Scots pine (Rebetez & Dobbertin 2004, Weber et al. 2005b, Zweifel et al. 2005, Bigler et al. in press). As a consequence, \( k_{DrT} \) of pubescent oak was set to 0.39, i.e. slightly higher than the value of Scots pine.

In contrast to earlier studies with ForClim, maximum tree height \( k_{HMax} \) and maximum tree age \( k_{AMax} \) were treated as being region-specific here. Trees at extreme sites with rather dry and shallow soils, such as those in the low-elevation forests of Valais, usually do not exceed a certain low stature. This was also the case for our sample plots, where tree height stayed always below 20 m (cf. Weber et al. 2005a). \( k_{HMax} \) was consequently adjusted to 20 m for both species. For \( k_{AMax} \), we could not rely on our field data because the measured maximum tree age in these formerly heavily exploited forests did not exceed 200 years. Nevertheless, pubescent oak was estimated to reach a higher potential age \( k_{AMax} \) with 500 years than Scots pine with 400 years, due to the higher resistance of oak wood as well as the higher pathogen pressure on pine particularly at warm sites, and because later successional tree species are supposed to reach a higher age from a theoretical point of view. Pine’s \( k_{AMax} \) was thus corrected down from the original value (760 years), which had been estimated from a global database of this widely distributed species. The \( kS \) parameter was reset to 90 for both species, i.e. Scots pine and pubescent oak were assumed to show the same initial height-diameter ratio in their growth.

**Model sensitivity to the new parameterisation**

For each newly estimated species parameter (excluding \( k_{HMax}, k_{AMax} \) and \( kS \)), we defined a range of plausibility, resulting in 14 parameter sets (including the default value; cf. Table 1). The model ForClim was run with Scots pine and pubescent oak only, for the Sion site (latitude 46°2’N, soil water holding capacity of 150 mm). On 200 patches of 1/12 ha, forest development was simulated over 400 years starting from bare ground with 25-year monitoring.
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This procedure was repeated for the 14 different parameter sets to evaluate the sensitivity of the model with respect to $kBrow$, $kLy$, $kDrT$ and $kLa$. Only one parameter was changed at a time. The resulting development of Scots pine and pubescent oak biomass over time was compared for the different parameter sets.

Table 1. Estimated default values (italic) and plausibility ranges of species parameters $kBrow$, $kLy$, $kDrT$ and $kLa$ for Scots pine and pubescent oak. These represent the 14 parameter sets used for the sensitivity analysis (only one parameter was changed at one time).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Oak</th>
<th>Pine</th>
</tr>
</thead>
<tbody>
<tr>
<td>Min</td>
<td>0.06</td>
<td>-</td>
</tr>
<tr>
<td>$kBrow$</td>
<td>0.1</td>
<td>0.01</td>
</tr>
<tr>
<td>Max</td>
<td>0.14</td>
<td>0.06</td>
</tr>
<tr>
<td>Min</td>
<td>0.05</td>
<td>0.3</td>
</tr>
<tr>
<td>$kLy$</td>
<td>0.1</td>
<td>0.4</td>
</tr>
<tr>
<td>Max</td>
<td>0.2</td>
<td>0.5</td>
</tr>
<tr>
<td>Min</td>
<td>0.37</td>
<td>0.35</td>
</tr>
<tr>
<td>$kDrT$</td>
<td>0.39</td>
<td>0.37</td>
</tr>
<tr>
<td>Max</td>
<td>0.41</td>
<td>0.39</td>
</tr>
<tr>
<td>Min</td>
<td>5</td>
<td>-</td>
</tr>
<tr>
<td>$kLa$</td>
<td>6</td>
<td>9</td>
</tr>
<tr>
<td>Max</td>
<td>7</td>
<td>-</td>
</tr>
</tbody>
</table>

Model sensitivity to grazing

In ForClim, the influence of grazing on forest succession is incorporated via the establishment submodule. The model allows for exploring the possible effects of varying browsing intensities on sapling establishment rates via the establishment filter $gBFlag$:

$$gBFlag = \begin{cases} 
0 & U(0,1) < gBrP = kBrow \cdot uBrPr \\
1 & \text{else}
\end{cases}$$

$gBFlag$ is a boolean auxiliary variable that allows (value = 1) or prevents (value = 0) establishment. Browsing pressure $uBrPr$ can be chosen on a nominal scale between 0 (no browsing) and 10 (heavy browsing), the standard value is 1 (Fig. 2). The species-specific browsing susceptibility parameter $kBrow$ represents annual browsing incidence as a fraction...
of the sapling population. $U(0,1)$ is a random number with a uniform distribution in the range [0...1]. The resulting maximum sapling mortality cannot exceed 100% (Fig. 2).

The uncertainty in the parameter estimates for $kBrow$ has been particularly high, and the reaction of the model to species-specific differences in this parameter has not been analysed so far. Therefore, the influence of various browsing susceptibilities of pubescent oak ($kBrowQ$) and Scots pine ($kBrowP$) on the behaviour of the model was examined in more detail by a systematic sensitivity analysis for quotients $kBrowQ/kBrowP$ with the values 1 (0.01/0.01), 6 (0.06/0.01) and 10 (0.1/0.01). In addition, five different browsing intensities $uBrPr$ (0.1, 1, 5, 9, 10) were applied. Simulated biomass for oak and pine were compared at an early (after 150 simulation years) and at a later successional stage (after 400 years).

Grazing scenario
The grazing scenario was set up based on our knowledge of historical land-use practices in the low-elevation forests of Valais. From historical sources and according to their stand age (Weber et al. 2005a), most of the current low-elevated forests initially established in the first half of the 19th century. At that time, large parts of the formerly forested area had been devastated by foreign armies and by local communities to extract export timber, firewood and railway timber (Meyer 1950, 1951, 1952, Kempf & Scherrer 1982), and they were thus predisposed for re-colonisation. Goat grazing had, for a long time, been a widespread practice in these forests (Stuber & Bürgi 2001) and ceased only after 1950, when goat numbers in Valais dropped from more than 30,000 (1950) to less than 6,000 (1970) (Ritzmann-Blickenstorfer 1996).

For the grazing scenario, we thus assumed that browsing pressure was very high ($uBrPr = 9$) for the first 150 years of succession and was normal ($uBrPr = 1$) during the next 250 years, corresponding to current conditions. Forest succession with and without (i.e. $uBrPr = 1$) the grazing scenario was simulated on 200 patches of 452.4 m², equivalent to the plot size of the field sites.

In this way, simulated stem numbers and basal areas with and without the grazing scenario could be compared directly with field records. For this comparison, an early successional stage (i.e. after 150 years of simulation) and a late successional stage (i.e. after 400 years of simulation) were chosen.
Results

Parameterisation of Scots pine and pubescent oak

Overall, the new local default parameterisation of Scots pine and pubescent oak resulted in a rather different development of species composition for the Sion site. Whereas the original parameterisation in ForClim V2.9.3 had produced stands with two times higher biomasses (>200 t/ha, results not shown) that were composed mainly of Scots pine, the new parameterisation resulted in mixed stands composed of about two thirds pubescent oak (around 70 t/ha) and one third Scots pine (around 40 t/ha) at a later successional stage (Fig. 3). Nevertheless, as a consequence of the lower maximum tree height, the simulated total stem number was about as high (1,000 stems/ha) as in the original model version.

The biomass of both species was found to react most sensitively to the drought tolerance parameter $k_{DrT}$. Pubescent oak had higher biomass than Scots pine only in cases where its $k_{DrT}$ was higher ($\geq 0.39$) than that of Scots pine (0.37). While the biomass of pubescent oak was most sensitive to the value of its own $k_{DrT}$ parameter, the development of Scots pine as a light demanding species ($k_{La} = 9$) depended also strongly on the parameterisation of pubescent oak ($k_{DrTQ}$ and $k_{LaQ}$). For Scots pine, the parameter incorporating the light requirement for establishment, $k_{Ly}$, had quite a strong influence on the later succession as well. At a higher light demand ($k_{Ly} = 0.5$), about 25% less biomass was produced. Unlike the establishment of pubescent oaks, the establishment of Scots pines was significantly restricted due to poorer light conditions after 400 years of succession. The number of establishing pine saplings was reduced by 60 up to 90%, the latter at an all-sided leaf area index (LAI) greater than 7, which was reached in the case of a very high $k_{DrT}$ of pubescent oak (0.41) (Fig. 3c). Because the number of newly established saplings was coupled to $k_{La}$, Scots pine was found to depend to a minor part also on $k_{La}$ of the competing oaks. Species-specific differences in the browsing susceptibility $kBrow$ played virtually no role at the standard grazing level ($u_{BrPr} = 1$).
Fig. 3. Simulation of biomass development over the first 400 years of succession using 14 different parameter sets for Scots pine (a) and pubescent oak (b). The development of the leaf area index (LAI) is shown in (c). The thick black curve belongs to the reference parameter set (Ref). $k_{BrOw}$: browsing susceptibility; $k_{Ly}$: light requirement of saplings; $k_{DrT}$: drought tolerance; $k_{La}$: light requirement of adult trees.

**Model sensitivity to grazing**

At grazing intensities that are higher than the standard value of 1 for the parameter $u_{BrPr}$, variations in the browsing susceptibility of pubescent oak relative to Scots pine (ratio $k_{BrOw}/k_{BrPr}$) were significantly changing the biomass and stem number relationships between oak and pine (Fig. 4), whereas under the standard value of $u_{BrPr}$ and even more so
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under a reduction of $u_{BrPr}$, biomass and tree numbers of the two species were little affected by changes in the relative browsing susceptibility of the two species.

![Diagram](image)

Fig. 4. Model behaviour for browsing intensities ($u_{BrPr}$) from 0.1 (hardly any browsing) to 10 (heavy browsing), 1 is the standard value. A browsing intensity of 9 was used in the grazing scenario. With increasing browsing pressure ($u_{BrPr}$), the portion of pubescent oak biomass (a,c) and stem number (b,d) decreases compared to Scots pine in the cases where oak is more susceptible to browsing than pine ($kBrowQ/kBrowP > 1$).

The more browsing susceptible pubescent oak was assumed to be relative to Scots pine, the smaller was the proportion of pubescent oak with respect to aboveground biomass (Figs. 4a,c) and stem numbers (Figs. 4b,d). For the original parameterisation of $kBrow$ ($kBrowQ/kBrowP = 6$), browsing decreased the proportion of pubescent oak already strongly, e.g. to only about 40% of the biomass of Scots pine at the early successional stage (Fig. 4a), if browsing pressure was high ($u_{BrPr} = 9$). At a half-way increased grazing intensity ($u_{BrPr} = 5$, cf. Fig. 2), the relative biomass of oak decreased by a factor two if pubescent oak was parameterised to be ten times more susceptible to browsing than Scots pine (Figs. 4a,c). For the same $kBrowQ/kBrowP$ ratio ($0.1/0.01 = 10$), pubescent oak disappeared completely at the highest possible grazing level ($u_{BrPr} = 10$). However, without grazing ($u_{BrPr} \leq 1$), pubescent oak
produced about twice the biomass and stem numbers of Scots pine after 400 years of succession (Figs. 4c,d).

**Comparison of field data with model results**

Before performing simulations with a realistic grazing scenario, tree density and basal area simulated by the model were compared with empirical data from the eight forest plots (Fig. 5). Simulated early and late successional tree densities of Scots pine under the standard grazing pressure (i.e. no enhanced grazing) were found to be near the upper and lower quartile limits of the empirical data (Fig. 5a), but most of the observed plot data were closer to the late successional stage in the model. For this stage, simulated pine tree density was only about half as high as simulated pubescent oak tree density. For pubescent oak, simulated tree density did not vary much with time, but it was slightly higher at the late successional stage. The median of the oak densities recorded in the field was quite close to the simulated tree densities, although some of the sampled plots had much higher densities.

![Boxplots of empirical tree density (a) and basal area (b) of eight plots in Valais compared to simulated stem numbers and basal areas at an early successional stage (after 150 years, grey bars) and at a later successional stage (after 400 years, black bars) for the reference parameter set, without enhanced grazing.](image)

Without enhanced grazing, simulated Scots pine basal area was significantly underestimated as measured by the basal area range of the eight sample plots in the low-elevation forests of Valais (Fig. 5b). By comparison, the recorded pubescent oak basal area corresponded in
average to the simulated basal area after 400 years of succession. The basal area simulated for
the early successional stage was within the interquartile range of the empirical data as well.

Applying the grazing scenario resulted in a rather different development of basal area over
time (Fig. 6). After the 150 years of intense grazing, Scots pine had reached a basal area about
a quarter higher than without enhanced grazing. Even after the cessation of heavy browsing,
basal area continued to grow for another 100 years, peaking at 16 m²/ha, i.e. in the range of
the empirical data.

Fig. 6. Development of Scots pine (top) and pubescent oak (bottom) basal area over time as simulated by
ForClim. Simulations were run with (solid) and without (dashed) the grazing scenario. The grazing scenario
includes 150 years of heavy browsing at the beginning (BrPr = 9) and 250 years without unusually high
browsing afterwards (BrPr = 1). The grey bars show the interquartile ranges of the empirical data.
According to our expectations, pubescent oak basal area remained low during the period of heavy grazing in the first 150 years of the simulated succession. Across the following 250 years without grazing, pubescent oak basal area increased nearly to the same level as in the succession simulated under the standard grazing intensity. The basal area curve of pubescent oak without intensive grazing entered the range of empirical data around 200 years earlier than the curve under the grazing scenario.

Discussion

Earlier applications of forest gap models for the low-elevation sites in Valais have resulted in forest types that were fairly different from field observation in that total biomass was overestimated and species composition was not realistic (Kienast & Kuhn 1989, Bugmann 1996, Bugmann & Cramer 1998). By adapting the ForClim model based on an improved knowledge of the autecology of Scots pine and pubescent oak, and by applying a grazing scenario based on land-use history, we arrived at a revealing simulation of forest development at these rather extreme sites. Without intensive grazing, simulated Scots pine basal area was underestimated compared to the empirical data (Fig. 5). By applying the grazing scenario, simulated Scots pine basal area peaked not only at a higher level, but also in the range of our field data (Figs. 5 and 6).

However, basal area of pubescent oak reached the range of the field data only 150 years after the cessation of heavy browsing (Fig. 6). Moreover, only after around 300 years of succession was there a short period, in which the simulated curves of both species were within the range of the empirical data. Thus, even though the general pattern was found to be realistic, the speed of the simulated succession was not consistent with historical sources and current field data. We can provide three possible explanations for this that are based on the forest history of the area or on model-internal limitations. First, it is not exactly known how long and how intensively these forest stands were grazed: a shorter period of intensive grazing would have led to a higher oak abundance in the model earlier in time. Second, a less intense grazing scenario than the one we assumed for the first phase would enhance oak regeneration, resulting in a higher oak abundance already during the early succession, so that measured oak levels would be attained more quickly after the abandonment of grazing. Third, the model
may generally underestimate the rate of succession because of an underestimation of the rates of establishment, growth or mortality.

The site-specific adaptation of the parameterisation alone was insufficient to simulate the current species composition (Fig. 5). Only by retarding the succession by increasing the browsing pressure for the first 150 years of the simulation (Fig. 6) were we able to explain why the observed Scots pine basal area in Valais is higher than we would expect it to be under natural conditions. Our modelling results suggest that succession is retarded considerably as long as heavy browsing pressure is present. The ultimate result is a longer period of codominance of the fairly browsing-tolerant, early successional Scots pine with the browsing-intolerant, late successional pubescent oak after the cessation of intense grazing. It is noteworthy that Seagle and Liang (2001) found the contrary, i.e. that succession was accelerated when regeneration and growth of the here preferentially browsed early successional species was reduced. Although in our case heavy browsing prevented the succession at the beginning, it probably permitted a longer phase of coexistence afterwards. This pattern may also be explained by a reduction of the dominance (Wohlgemuth et al. 2002) of the later successional species by grazing.

Our results thus suggest that past forest use practices have favoured the regeneration and growth of Scots pine and inhibited the regeneration of pubescent oak, while currently Scots pine is at least partly being displaced by pubescent oak. Processes similar to those in Valais have been studied in Scots pine stands that are managed no longer in The Netherlands. Massive natural regeneration of broad-leaved trees has been reported in many of these ageing stands, and the application of a model with special emphasis on the recruitment of oaks (*Quercus robur* and *Q. petraea*) resulted in similar pathways of stand development as in our study (Kint et al. 2004). Simulating Mediterranean mixed Aleppo pine (drought tolerant) and Holm oak (less drought tolerant) in a mesic homogeneous forest, Zavala *et al.* (2004) showed that pines were generally able to dominate longer when their colonisation-competition trade-off was favoured by disturbances. These processes are also supported by the observation of similar developments from pine towards oak dominated stands in forests formerly used for grazing, e.g. for *Pinus densiflora* and *Quercus* spp. in Korea (Beon & Bartsch 2003).

In all the above cases, the establishment ability of the two involved species plays a major role for the trajectories of the simulated and observed forest succession. Concerning grazing, we
therefore need accurate data on the relative browsing susceptibilities ($kBrow$) of the tree species involved. Improved knowledge in this respect will help to evaluate which species are browsed preferentially when they occur together, and which ones will be browsed only if browsing pressure is high and no species with higher browsing susceptibility occurs for other reasons. For example, we know that pine is more strongly browsed at other locations than in Valais, e.g. in Scottish (Palmer & Truscott 2003) or Dutch pinewoods (Jorritsma et al. 1999).

Besides the sensitivity to the $kBrow$ parameter (Fig. 4), the model reacted also in a sensitive manner to the drought tolerance parameter $kDrT$ (Fig. 3). Scots pine recruitment was affected strongly by the higher biomass of the comparably more drought tolerant pubescent oak, which restricted the establishment of Scots pine saplings due to decreased light availability at the forest floor (Fig. 3c). Drought is thought to be an ultimate constraint on the distribution and abundance of plants (Hanson & Weltzin 2000), although it is believed to exert rather a direct abiotic than an indirect biotic influence on species regeneration and growth. Such influences will have to be investigated further and will help to improve the behaviour of forest models at extremely dry sites by the integration of modified drought response functions.

Even though the modelling study presented here lacks a proper model validation, the results suggest that the knowledge of past and present anthropogenic impacts on forests and their integration in forest models can provide novel insights and deserve further investigation. The impacts of a changing climate on forests in Switzerland have been evaluated in a relatively detailed manner using forest gap models (Kräuchi & Kienast 1993, Kienast et al. 1996, Bugmann 1997, Fischlin & Gyalistras 1997). However, changes in land-use, which has been the main driver of forest dynamics in many stands for hundreds of years, may have an even greater impact on forest succession. One has to be aware that the effects of climate change could therefore be masked by the effects of land-use change (cf. Motta & Edouard 2005), and both drivers should be included in future investigations.

Our study suggests that even with simple assumptions about past grazing rates and simple formulations of the effects of grazing, the realism of forest gap models can be increased considerably. Particularly in regions that are characterised by a long history of forest grazing and other widespread forest-use practices such as timber harvesting and litter clearance (Badeck et al. 2001), model projections should include these uses instead of relaying on constructs such as the potential natural vegetation alone.
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Chapter IV

Growth reactions of *Pinus sylvestris* L. and *Quercus pubescens* Willd. to drought years at a xeric site in Valais, Switzerland

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¹Swiss Federal Institute for Forest, Snow and Landscape Research, WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland
²University of Hamburg, Department for Wood Science, Division of Wood Biology; Leuschnerstrasse 91, D-21031 Hamburg, Germany
³Forest Ecology, Department of Environmental Sciences, Swiss Federal Institute of Technology, CH-8092 Zurich, Switzerland

Abstract

In Valais, an inner-Alpine dry valley in Switzerland, low-elevation Scots pine (*Pinus sylvestris* L.) forests are changing. While pine shows high mortality rates, deciduous species, in particular pubescent oak (*Quercus pubescens* Willd.), are becoming more abundant. We hypothesise that increasing drought and the species-specific drought tolerance are key factors in these processes. In this study, the growth reaction to drought years of pine and oak growing on a xeric site in Valais was analysed using dendrochronological and wood anatomical methods. Congruent with theoretical expectations, the tree-ring widths of both species, the mean lumen area of earlywood vessels in oak and the radial number of tracheids in pine decreased in response to dry conditions. However, both species also showed reactions deviating from those at mesic sites: In oak, the mean lumen area of latewood vessels increased in drought years. In the driest year of the period (1976), the mean radial diameter of pine increased in latewood and decreased only slightly in earlywood. These results emphasise that the process of wood formation and cell functionality on xeric sites is not completely understood yet. Both species seem to have difficulties to adapt the size of their water-
conducting cells to strongly reduced water availability in drought years. Additionally, the cell number is strongly reduced. Thus it remains unclear if both species can maintain sufficient water transport under increasingly dry conditions.

**Keywords**: ecological wood anatomy; dendroecology; vessel size; radial tracheid diameter; climate change

**Introduction**

In Valais, an inner-Alpine dry valley in Switzerland, a high mortality of Scots pine (*Pinus sylvestris* L.) has been observed in the last century and especially since the beginning of the 1990s (Rigling & Cherubini 1999, Rigling et al. 2004). Simultaneously, deciduous trees, in particular the sub-Mediterranean pubescent oak (*Quercus pubescens* Willd.) are becoming more abundant. On dry, low elevation sites, oak is increasingly competing with pine. According to Rebetez and Dobbertin (2004) and Begert et al. (2005), the temperature in Valais has risen significantly during the past decades. Together with a constant precipitation regime (Begert et al., 2005), this aggravates the problem of water availability for plants by increasing évapotranspiration. Land-use changes and the direct and indirect influence of climate warming, such as drought, insects and phytopathogens, are thought to act as key factors in pine mortality and changes of the species composition (Rigling & Cherubini 1999, Rebetez & Dobbertin 2004).

Dendroecological methods have frequently been used to analyse climate-growth relationships of Scots pine and pubescent oak on dry sites (Kienast et al. 1987, Tessier et al. 1994, Rigling et al. 2001, Rigling et al. 2002, Cherubini et al. 2003, Rigling et al. 2003, Weber et al. 2005, Bigler et al. in press). In the driest summer months, the growth of pine strongly depends on how much water is available, while oak is less dependent on water availability because of its ability to stop growing (Cherubini et al., 2003).

Tree-ring width is influenced by the climate of both the current and previous years, thus often leading to climate-growth relationships that are difficult to interpret (Fritts 1976, Schweingruber 1983). The separation of the growth rings into earlywood and latewood may lead to a higher resolution regarding the climatic forcing, but the influence of the previous
year is still relevant (Eckstein & Schmidt 1974). Wood anatomical features such as cell size or number of cells seem to be more directly linked with the climatic conditions at the time of cell division and cell enlargement than tree-ring width (Woodcock 1989, Vaganov 1990). Thus, cells can be seen as climate archives with a high temporal resolution. For example, cell size is mainly controlled by water availability at the time of cell enlargement. Hence, cell size should decrease when water availability is low (Vaganov 1990, Dünisch & Bauch 1994a, Sass & Eckstein 1995, Pumijumnong & Park 1999, Gonzalez & Eckstein 2003), and variations in cell size allow for estimating water, but also mineral supply of a tree, because an increase in cell size causes an increase in cell water conductivity to the power of four (Hagen Poiseuille law, Tyree & Zimmermann 2002). However, at the wood anatomical level, the growth reactions of pine and oak to drought years have systematically been analysed only at mesic sites so far (Knigge & Schulz 1961, Park 2000).

The aim of this study, therefore, was to analyse the growth reactions to drought years of Scots pine and pubescent oak at a xeric site in Valais using a combination of dendroecological and wood anatomical methods. We focus on differences in the reaction of tree-ring width and the number and size of water conducting cells such as tracheids and vessels between drought and mesic years. With this study, we want to evaluate i) whether oak is less affected by drought years than pine due to its advantageous conducting system and ii) whether pine and oak at a xeric site react in a similar manner to drought years, i.e. by reducing their ring-width, cell number and cell size, as at mesic sites.

**Materials and Methods**

**Study site**

The study site is located in the Swiss Rhône valley in Valais (Fig. 1), one of the driest regions of the Central Alps (Ozenda 1985). The study plot is situated in the dry central part of Valais, near the village of Salgesch. The most important characteristics of the study site are summarised in Table 1.
Table 1. Characteristics of the study area.

<table>
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<tr>
<th>Location</th>
<th>46°19'0&quot;N; 7°33'40&quot;E</th>
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<tbody>
<tr>
<td>Altitude</td>
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<td>Aspect</td>
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<tr>
<td>Soil type</td>
<td>Rendzic leptosol</td>
</tr>
<tr>
<td>Field capacity</td>
<td>60 to 97 mm</td>
</tr>
<tr>
<td>Duration of sunshine</td>
<td>2,094 h/a</td>
</tr>
<tr>
<td>Degree of tree cover</td>
<td>70 to 80 %</td>
</tr>
<tr>
<td>Maximum tree height</td>
<td>14 m</td>
</tr>
</tbody>
</table>

Monthly precipitation data (1910-2002) were obtained from the meteorological station at Sierre, 5 km from the study site. Because this station does not record temperature, monthly temperature data (1910-2002) were taken from the station at Sion, 20 km from the study site. Annual rainfall amounts to 664 mm, and annual mean temperature is about 9.2 °C (Fig. 2).

During summer, drought periods can last for several weeks and occur nearly every year (Kuhn 1973). Most of the summer precipitation events bring less than 2 mm rain (Burnand
1976). Taking into account interception losses, only very little of this rainfall is actually available for tree growth (Kuhn 1973). In addition, these low rainfall conditions are amplified by high insolation and a low incidence of clouds and fog (Burnand 1976).

To quantify drought conditions, we calculated the monthly drought index according to Bigler et al. (in press), which is defined as the difference between monthly precipitation and the monthly potential evapotranspiration according to Thornthwaite (1948). An annual drought index was calculated as the sum of the monthly index values from September of the previous year to August of the current year. Drought and mesic years are characterized by negative and positive values of the annual drought index, respectively.

The forest association has elements of the Ononido-Pinetum (Plumettaz Clot 1988) and the Saponario-Quercetum pubescentis (Burnand 1976) with Scots pine and pubescent oak as the main tree species. In Valais, the distribution ranges of the two species overlap. Scots pine is a sub-boreal species with a wide ecological amplitude (Burnand 1976). As a typical pioneer tree species, pine needs light for germination and growth and thus is less competitive in mixed stands (Landolt 1977). Pubescent oak is a sub-Mediterranean tree species that requires high temperatures and is very sensitive to late frost (Burnand 1976). In general, both species are known to be relatively well-adapted to drought (Ellenberg 1986).

**Sampling and dendrochronological investigations**

Sampling was carried out in June 2003. We randomly chose 21 dominant or co-dominant trees per species. Two increment cores were taken from each tree at breast height (1.3 m). Diameter at breast height, tree height and any visible damage (e.g. by insects or infection with mistletoes) were recorded.

Tree-ring width was measured using a combination of a Lintab digital positioning table and the Time Series Analysis Program TSAP (both Rinntech Heidelberg/Germany). Because of numerous missing or discontinuous rings and density fluctuations, cross-dating was not always possible. Therefore, only 13 oaks and 11 pines could be included in the analysis. Standard statistics such as first order autocorrelation and the mean sensitivity of the raw tree-ring series were computed.
To eliminate the individual growth trends, double detrending was applied using the software ARSTAN (Holmes 1994). In a first step, we fitted a negative exponential curve (Fritts 1976) and then a cubic smoothing spline with a 50% frequency response of 128 years (Cook & Peters 1981) to each single tree-ring series. The detrended indexed series were then averaged to the standard chronology by a robust biweight mean. The relationship between the ring-width indices and the annual drought index was calculated using Pearson correlations.

**Wood anatomical investigations**

The wood anatomical investigations were based on a sub-sample of 10 oaks and 9 pines, which fitted best with the tree-ring width of the standard chronologies. From each tree, one core was analysed. The analysis of the anatomical parameters was performed on a 16-year sequence, from 1970 to 1985. This period contains three drought years (1972, 1974, 1976) including 1976, one of the driest in the last century, and three mesic years (1977, 1978, 1980), allowing for the analysis of wood anatomical parameters in drought years without a growth trend caused by cambial age (Gasson 1987, Park 2000).

The growth rings of this period were separated from the cores, and cross-sections with thicknesses of 10 µm (pubescent oak) and 20 µm (Scots pine) were cut using a sliding microtome (Reichert, Germany). For a better differentiation of the tissue, the sections were stained with safranin and astrablue, dehydrated with alcohol and xylol, and mounted with Canada balsam. Using a CCD video camera installed on an optical microscope (Aristoplan, Leitz, Wetzlar/Germany) and connected with a computer, pictures of the cross-sections were taken with a magnification of x40 (oak) or x100 (pine). The anatomical parameters were measured using the image analysis software “Image Pro Plus” Version 1.3 (Media Cybernetics, Silver Spring/USA).

**Pubescent oak**: The lumen area of earlywood and latewood vessels was measured for each single year in a window of 2.4 mm tangential width. The classification into earlywood and latewood vessels was performed using threshold values: Vessels with a lumen area between 450 and 5,000 µm² were defined as latewood vessels; those with a lumen area greater than 5,000 µm² were defined as earlywood vessels. Structures such as large axial or ray-parenchyma cells were manually excluded from the measurements. Mean annual values for earlywood and latewood vessel lumen areas and the double standard error were calculated.
Additionally, the number of measured vessels and their classification into earlywood vs. latewood were recorded, and the frequency distribution of latewood vessels was calculated.

_Scots pine:_ We focussed on the radial diameter and the number of tracheids. The lumen areas of five radial cell rows per growth ring were measured from earlywood to latewood (Fig. 3a). Only those rows were chosen where the tracheids were cut approximately in the middle of their length (i.e., the cells where the tangential and radial diameter became maximal). Three tangential diameters per row (in the first and last cell and one in the middle part of the row) were measured manually. A mean tangential diameter was then calculated for each cell row. The tracheid lumen areas were divided by the mean tangential diameter to get an estimate of the radial diameter of each cell. Like this, we derived a curve of the radial cell diameters from the first earlywood to the last latewood cell of one cell row.

Fig. 3. Cross-section of a tree-ring of Scots pine; measured tracheid file with grey-coloured cell lumen (a); smoothed average curve of the radial diameter (b); black lines mark the determined border between earlywood, transition wood and latewood in b.

The curves of the radial diameter of the five measured cell rows were averaged to a mean curve. This mean curve was smoothed by a moving average with a running window of five cells. The curve progression of this smoothed average (Fig. 3b) remained relatively constant at a high level in the earlywood, declined rapidly in the transition wood and showed an asymptotic course in the latewood. Because we were interested in analysing the reaction of the different functional tissues to drought, we wanted to separate latewood with mainly
mechanical function from earlywood and transition wood with a mainly water-conducting function (Bosshard 1982). To delimit these tissues we calculated the slope of the smoothed average curve: The point where the slope first showed a value less than minus one was defined as the border between earlywood and transition wood (Fig. 3b: cell number 4). The point where the slope took again a value greater than minus one was defined as the border between transition wood and latewood (Fig. 3b: cell number 12).

Mean values for the earlywood and latewood diameters and their double standard errors were calculated. In addition, the overall mean annual number of cells and its standard error was calculated, and the fraction of earlywood vs. latewood cells was recorded.

Results

Dendrochronology

The chronologies of the standardized tree-ring width of oak and pine was correlated strongly with the annual drought index \( r_{\text{oak}} = 0.58, p < 0.001; \ r_{\text{pine}} = 0.34; p < 0.001 \) in the years 1910 to 2002 (Fig. 4). Extreme drought years such as 1921, 1933, 1934, 1944, 1949, 1954, 1976 and 1998 coincided with a sharp reduction of tree-ring width. The pattern of the annual increments of oak and pine were quite similar \( r = 0.44; p < 0.001 \).

The first order autocorrelation (Table 2), which describes the influence of the previous growth on the growth of the current year (Fritts 1976), was rather low for both species, but pines showed higher values than oak. The mean sensitivity (Table 2), which describes the relative variability in the widths of adjacent growth rings (Fritts 1976), was high for both species, though oak reacted more sensitively than pine.
Table 2. Descriptive statistics of the dendrochronological investigations. First order autocorrelation, mean sensitivity and Gleichläufigkeit were calculated from the standardised tree-ring chronologies. “Gleichläufigkeit” is a measure of the year-to-year agreement between the interval trends of two chronologies based upon the sign of agreement, usually expressed as a percentage of cases of agreement. (Schweingruber 1982). Gleichläufigkeit was calculated between standardised tree-ring chronologies and the annual drought index. Mean increment and standard deviation were calculated from the raw tree-ring chronology.

<table>
<thead>
<tr>
<th>Pubescent oak</th>
<th>Scots pine</th>
</tr>
</thead>
<tbody>
<tr>
<td>First order autocorrelation</td>
<td>0.27</td>
</tr>
<tr>
<td>Mean sensitivity</td>
<td>0.32</td>
</tr>
<tr>
<td>“Gleichläufigkeit” [%]</td>
<td>68</td>
</tr>
<tr>
<td>Mean increment [mm]</td>
<td>0.80</td>
</tr>
<tr>
<td>Standard deviation [mm]</td>
<td>0.24</td>
</tr>
</tbody>
</table>

**Wood anatomy**

The first half of the period of interest for the wood anatomical investigations (1970-1985) is characterised by three drought years, 1972, 1974 and 1976. The second half of the period includes three mesic years, 1977, 1978 and 1980. The driest year of the period is 1976, characterized by exceptionally dry conditions from December to June. Even though the
conditions were getting wetter in July, it is doubtful that this affected tree growth positively, because it is likely that in a drought year the cell formation ceases prematurely by the end of June (Larson 1962, Denne & Dodd 1981).

*Pubescent oak:* The curves of the lumen area of the earlywood vessels and of the drought index (Fig. 5a) correlated slightly (Glm = 67%; r = 0.31; p < 0.1). In drought years, the mean lumen area of earlywood vessels generally decreased. When conditions became better in the succeeding year (e.g. 1975), the mean lumen area of earlywood vessels increased, except in 1977 where the curve showed a further decline even though the climatic conditions were much better than in the extreme drought year 1976. In contrast, the mean lumen area of latewood vessels and the drought index were correlated negatively (Glm = 2%; r = -0.26; n.s.) (Fig. 5b).

![Fig. 5. Mean lumen area (black curve) of earlywood (a) and latewood (b) vessels of pubescent oak with the double standard error and the annual drought index (grey curve).](image)

To reveal how the mean lumen area of latewood vessels was composed, we analyzed the vessel size frequency distribution (histograms). Figure 6 contrasts the histograms of three drought years with three mesic years, showing differences mainly in the proportion of small vessels (< 2,000 μm²). The wide tree-rings in mesic years contain a higher number of small latewood vessels, but the proportion of large latewood vessels was similar to that of narrow rings in the dry years.
By comparing the number of vessels in earlywood and latewood with the annual drought index (Fig. 7), it became apparent that it was mainly the number of latewood vessels that decreased in drought years. Hence, the number of latewood vessels was correlated highly significantly with the drought index (Glg = 87%; r = 0.82; p < 0.001), whereas the number of earlywood vessels varied only little over the years and showed no significant correlation with the drought index (Glg 46%; r = -0.12; n.s.).
Fig. 7. Number of earlywood (grey bars; mean standard error = 2.42) and latewood vessels (black bars; mean standard error = 36.45) of pubescent oak averaged over all trees per year and the annual drought index (grey curve).

*Scots pine*: The mean number of cells per year showed a similar development as the annual drought index (Glk 80%; r = 0.53; p < 0.05) (Fig. 8a). The separation into earlywood and latewood (Fig. 8b) demonstrates that the two components of the growth ring reacted in different ways.

Fig. 8. Mean number of tracheids per year (black curve) of Scots pine with the standard error and the annual drought index (grey curve) (a); number of earlywood (grey bars; standard error = 5.63) and latewood tracheids (black bars; standard error = 3.52) averaged over all trees analysed per year and the annual drought index (grey curve) (b).
The mean number of cells correlated significantly with the drought index in latewood (Glive = 73%; r = 0.67; p < 0.05) but not in earlywood (Glive = 73%; r = 0.26; n.s.). Even though the lowest number of earlywood cells was produced in the drought year 1976, the reaction to drought was not very distinct. In the drought year 1972, no clear decline in the number of earlywood cells was evident, while in the mesic year 1973 a clear decline was visible.

The radial lumen diameter of earlywood tracheids was correlated slightly with the drought index (Glive= 53%; r = 0.45; p < 0.1) (Fig. 9a). Up to 1975, the curves coincided fairly well, whereas in the second part of the period, the common signal was low.

![Graph](image)

**Fig. 9.** Mean radial lumen diameter (black curve) of earlywood (a) and latewood (b) tracheids of Scots pine with the double standard error and the annual drought index (grey curve).

The mean lumen diameter decreased only slightly (especially in the drought year 1976), whereas the smallest lumen diameters occurred in the less dry year 1974. The mean lumen diameter of the latewood tracheids and the drought index did not correlate significantly (Glive = 73%; r = 0.36; n.s.) (Fig. 9b) except for the middle part of the period. The smallest lumen diameter occurred in the moderate year 1975, not in the drought year 1976.
Discussion

Dendrochronology

In drought years, the tree-ring width of both, pine and oak, was consistently reduced (Fig. 4), which is in accordance with other studies from inner-Alpine dry valleys (Kienast et al. 1987, Tessier et al. 1994, Oberhuber 2001, Rigling et al. 2002). The mean sensitivity of the pine chronology (Table 2) showed comparable values with other studies on dry sites (e.g. Oberhuber 2001, Rigling et al. 2002). In our study, oaks had a higher mean sensitivity than pine, and than oaks on more mesic sites, e.g. in Italy (Nola 1996, Cherubini et al. 2003).

The first order autocorrelation was noticeably higher for pine than for oak. This reflects the stronger influence of prior growth on the annual increment of pine, which could be caused by the longer life of the pine needles (1-5 years) (Kurkela & Jalkanen 1990) compared to the leaves of the deciduous oak. Other studies on dry sites (e.g. Oberhuber 2001, Rigling et al. 2002) showed similar first order autocorrelation for pine compared to our study. The first order autocorrelation of oak in our study was lower than at mesic sites (Nola 1996, Cherubini et al. 2003). This is in accordance with Fritts et al. (1965) and Rigling et al. (2002) who showed that the influence of prior growth is lower at xeric sites.

Wood anatomy

Pubescent oak: In agreement with the study of Gonzalez and Eckstein (2003), the mean lumen area of earlywood vessels was smaller in drought years than in mesic years (Fig. 4a). The vessel lumen area is an indicator of water availability at the time of cell differentiation (Sass & Eckstein 1995, Gonzalez & Eckstein 2003). Water availability and the osmotic conditions within the differentiating cells mainly control turgor pressure (Ray et al. 1972), which is one of the driving forces for cell enlargement (Boyer 1985) and thus involved in cell size determination.

Nevertheless, other studies of oak species have shown that the average size of earlywood vessels increased with increasing drought (for Quercus spp., cf. Knigge and Schulz (1961); for Quercus faginea Lam., cf. Concueria et al. (2004)) or varied only slightly when precipitation changed (for Quercus macrocarpa Michx., cf. Woodcock (1989)). Among the reasons for these discrepancies with our results may be the dissimilarity between the study
sites, the different species examined, the different growing conditions in the prior growth years, or a stronger internal control of earlywood formation (Woodcock 1989). In our study, the strong internal control of earlywood vessel formation was evident, as there were only slight changes in the annual number of earlywood vessels, in spite of highly variable climatic conditions (Fig. 7a).

In latewood, the increase of the mean vessel lumen area in drought years (Fig. 5b, 1972, 1974, 1976) resulted from the decrease of the number of small latewood vessels (< 2,000 μm²) (Fig. 6) due to the reduced latewood width (Fig. 7b). This implies that mean latewood vessel size alone is insufficient to analyse the reaction to drought.

In our study, the pattern of the frequency distribution of the latewood vessel areas did not change between drought and moderate years (Fig. 6). In contrast, Knigge and Schulz (1961) found a significantly higher proportion of small latewood vessels in drought years on a mesic site in Germany. The distribution pattern they found in a drought year corresponds exactly to the pattern in our study. In other words, on our dry study site in Valais wood formation corresponds to that of drought years on a mesic site in Germany. In a dry environment such as in Valais, pubescent oaks were reacting to additional, prolonged droughts by reducing their cell production, and not by adapting latewood vessel size.

**Scots pine:** In accordance with earlier studies on conifers (Zahner et al. 1964, Abe & Nakai 1999, Park 2000), the mean annual number of radial tracheid rows was lower in drought years than in mesic years (Fig. 8a). The climate sensitivity of cambial activity expressed by the annual variation of cell number may be explained by a reduction in mineral supply in the cambium due to the limited water uptake, the negative effect on protein metabolism (Larcher 1995), a reduction in the synthesis of growth regulators (Little & Savidge 1987) and the reduced assimilate availability, caused by decreasing photosynthetic activity (Hansen & Beck 1994).

The radial diameter of earlywood and latewood tracheids showed only a modest relationship with the drought index (Fig. 9), although in other studies it was found to be affected directly by changes in water availability at the time of cell enlargement, and therefore we expected that it should decrease with increasing drought (Sheriff & Whitehead 1984, Vaganov 1990, Dünisch & Bauch 1994a, Abe et al. 2003). However, this discrepancy may derive from a
methodological problem, because cells enlarge during a short time span of 10 to 30 days only (depending on the phase of the growing season), whereas we compared the final cell size with the annual mean of the drought index. For a more accurate analysis of climate-growth relationships, it would therefore be important to know the exact time of the cell enlarging period, but this is only possible by investigations on an intra-annual scale.

In the driest year of the study period (1976), tracheid diameter changes did not correspond with the magnitude of the prevailing drought. Earlywood diameter was only slightly reduced, and it remained constant in the latewood. Even though some inaccuracies might be expected, it seems reasonable to assume that on dry sites cell size is influenced by additional factors besides limited water availability in drought years. One of these factors could be the longer period of cell enlargement under dry conditions, as suggested by Moehring et al. (1975) and Dünisch and Bauch (1994a), which might lead to wider conduits (Wodzicki 1965, Aloni 1991). However, under drought conditions additional factors may override this influence, e.g. the limitation of assimilates and a reduced synthesis of growth regulators, which are essential for cell enlargement, by slackening the primary wall (Larson 1963, Dörfling 1986).

**Comparison of pubescent oak and Scots pine**

Even though it is difficult to compare ring-porous species with conifers, the responses to drought of oak and pine showed some similarities. In both species, the cambium reacted more sensitively to drought in the later part of the growing period than at the beginning, which is in accordance with other studies (Woodcock 1989, Sass & Eckstein 1995, Park 2000). The numbers of latewood tracheids or vessels were generally more strongly restricted by drought than the number of earlywood cells (Figs. 7b and 8b). In contrast, the number of earlywood vessels in oak varied only very little within the time period (Fig. 7a), which demonstrates a strong endogenous control of earlywood vessel formation.

Endogenous control is important in ring-porous trees like oak because the large earlywood vessels, where the main part of water transport occurs, cavitate in the same vegetation period in which they are built (Granier et al. 1994). A reduction in the number of earlywood vessels caused by exogenous factors would, therefore, have extensive implications for the physiological processes at the beginning of the growth period (Larcher 1984), such as bud break.
Both species showed reactions to drought unlike those described in other studies (Knigge & Schulz 1961, Woodcock 1989, Vaganov 1990, Abe & Nakai 1999, Park 2000, Corcuera et al. 2004). In oak, the pattern of the frequency distribution of latewood vessels did not vary between drought and mesic years, and in pine the mean radial diameter of earlywood and latewood tracheids did not show a clear response to the driest year of the investigated period (1976). These deviations are probably due to the extremely dry conditions under which the growth rate of both species was greatly reduced.

Effective water transport is particularly important when water availability is limited, such as in Valais. According to the Hagen-Poiseuille law, an increase in diameter causes an increase in cell conductivity to the fourth power (Tyree & Zimmermann 2002). Angiosperms are therefore in average able to conduct water 270% faster than conifers (Maherali et al. 2004). Hence, pubescent oak can react faster to a sudden increase of water availability than pine (Zimmermann & Brown 1971, Sperry 2003). Although oak has an advantage in its water-conducting system, our wood anatomical investigations indicate that both species are strongly limited in growth during drought years. Therefore, it is questionable if pine and oak can further adapt their water-conducting tissues to an expected drier climate.

Regarding cavitation, conifers are generally more resistant than angiosperms (Magnani et al. 2002). However, Pinaceae, specially Pinus, are more vulnerable than other conifers (Martinez-Vilalta et al. 2004). Furthermore, Scots pine is the only pine species that shows drought-induced mortality by hydraulic failure due to xylem embolism (Martinez-Vilalta & Pinol 2002). In contrast, pubescent oak showed a lower vulnerability to cavitation than other European deciduous oaks (Cochard et al. 1992, Nardini & Pitt 1999). However, in a case study from central Italy, pubescent oak was reported to operate at the limits of safety, whereby prolonged drought stress might lead to oak decline (Tognetti et al. 1998). Therefore, cavitation is an important factor for the survival of both species on dry sites.

In Valais, a significant warming during the past century is reported (Rebetez & Dobbertin 2004, Begert et al. 2005). The expected future warming (IPCC 2001) could aggravate drought conditions in Valais, which is likely to have negative effects on the growth and survival of oak and pine due to an increased risk of cavitation.
Conclusion

The growth reactions of pine and oak did not conform to our expectations: Both species are strongly affected by drought years. It remains unclear if oak can take an advantage of its superior conducting system. Even though cell number and tree-ring width were clearly reduced, both species showed deviating reactions in cell size from that described for mesic sites. This emphasises that the process of wood formation on dry sites is not understood in detail, yet. Further investigations should focus on intra-annual wood anatomical studies using, for example, the pinning method (e.g. Schmitt et al. 2004), which enables an accurate analysis of the climate-cell growth relationship with a high temporal resolution. In addition, controlled irrigation experiments would allow for a verification of the current theory about the influence of drought on cell division and differentiation.

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References


Chapter IV


**Synthesis**

The main objective of this thesis was to develop and apply a combination of different methods at different hierarchical levels (cf. Introduction, Fig. 1) to evaluate competition and stand dynamics of mixed Scots pine and pubescent oak stands as a scientific basis for forest management and conservation of the low-elevation forests in Valais.

This synthesis chapter is structured into four sections, whereof the first two address methodological issues, and the latter two discuss the results of this thesis with a focus on i) processes of change in the low-elevation Scots pine forests in Valais and ii) consequences for forest management and conservation.

**Studying forest dynamics from the cell to the stand level**

This section discusses the methodological approach adopted in the thesis to study competition and stand dynamics at different scales both in time and space (Fig. 1); I will highlight the major advantages of this approach and point out some difficulties.

To provide an overview of the findings of this thesis from a methodological point of view, each of the three main parts of the thesis will be described by the hierarchical levels addressed (Introduction, Fig. 1) and the methods used. Based upon this, I will answer the following questions: What did we achieve by combining different levels and by using different methods to cover different temporal and spatial scales?

**Autecology:** At the cell and tree-ring level, the high-frequency reactions of tree-ring width and cell structure to moisture availability were studied (chapters I and IV). Species-specific responses were analysed at the local and the regional scale. However, changes in the response to moisture availability were not evaluated over time, and reactions at the individual tree level were not analysed. With this approach, I attained a rather detailed understanding of the growth reaction to drought of Scots pine and pubescent oak, which could be interpreted in terms of physiological adaptations to the prevailing site conditions. The general result of species-specific differences in the drought response may even be applicable for a large-scale description of the ecology of Scots pine and pubescent oak in sub-continental, sub-Mediterranean climates.
Competition: The investigations of inter- and intraspecific competition were based on analyses at the tree level (chapter II), concentrating on interactions among individual trees. The short-term influence of climate on growth was not a main focus and was even partially removed by calculating bai ratios of neighbouring trees, due to the usually similar reactions of single trees to the local climate. Nevertheless, moisture availability was still found to play a role for such small-scale interspecific competitive processes (interval trends). By relating the retrospective dynamic competition index to sapwood area and to the proportion of dead branches, it could be shown that increasing competition for light can be important for Scots pine trees at the investigated sites. This conclusion was generated based on different competitive patterns as derived from all the trees of five low-elevation stands as a whole. It was therefore valid at the regional scale, but was not discussed in more detail at the stand level or even by following the fate of individual trees. In contrast to the autecological part, the competition part included a temporal perspective, as it was reconstructing competitive changes over a time window of 40 years.

Dynamic Model: The model application (chapter III) reflects our understanding of the forest dynamics at xeric low-elevation sites in Valais, since the model was used to integrate the main prevailing processes at these sites. The modelling study can be seen as a synthesis of our improved knowledge of the autecological properties and the competitive interactions between the two species, as well as a synthesis of the improved understanding of the driving forces for stand dynamics. Although the results obtained are strictly valid only at the stand level, we can cautiously generalise and extrapolate them to the regional level, at least for sites with similar conditions. Compared with the tree-ring data used in the dendroecological parts, the model output had a lower temporal resolution, in spite of the model calculating growth on an annual basis. In addition, forest composition after 200 years of succession in the model did not correspond to the empirical data. Therefore, a detailed model validation would be required to achieve a more accurate representation of forest development over time, including the use of tree-ring growth and weather data. Yet, the model application helped to improve our understanding of the long-term effect of grazing as a factor for forest succession, which was not feasible with the empirical data that covered a smaller time window.
From the above, it is evident that competition between Scots pine and pubescent oak was studied with a multi-scale approach, in both time and space (Fig. 1). Each level on its own and in combination with the others was needed to gain insight into the complex problem of growth and species composition of the forests in Valais. In the autecological part (chapter I), individual characteristics in the radial growth response to moisture availability were neglected. Therefore, it was important to integrate individual growth patterns by studying competitive interactions at the level of single trees (chapter II), thereby excluding the common climate signal. Although this approach enabled the tracing of competitive patterns 40 years back in time, the modelling study (chapter III) was needed to prolong the period of reconstructed forest development. Moreover, simulating forest succession helped to reveal the most important influencing factors for improving the knowledge of past and the prediction of future forest development. With the model, factors exerting a long-term effect could be determined, such as different browsing susceptibilities of Scots pine and pubescent oak in combination with past forest management. In addition, the wood anatomical study (chapter IV) provided a basis to explain physiological differences between the two species at the cell level.

In conclusion, by concentrating on a different level in each of the four parts of the thesis (Introduction, Fig. 1), I arrived at a rather broad but at the same time detailed understanding
of tree growth and forest succession in the low-elevation forests of Valais. However, the difficulty in this approach was to develop an adequate sampling design and to obtain data of sufficiently high quality for analysing research questions at different spatial and temporal scales. This is the usual dilemma of ecological studies (e.g. Smith & Urban 1988). In other words, data of a fine temporal resolution were required for chapters I, II and IV, whilst for chapters II and III they also needed to cover as long a period as possible. At the same time, the data ought to be general enough to represent the low-elevation forest type at xeric sites as a basis for chapter III. The sampling of trees old enough for calculating the drought response in chapter I was not always feasible inside the whole-stand plots as chosen for the competition analyses (chapter II). Consequently, the number of sites that could be used for the response function analysis in chapter I had to be reduced. On the other hand, sampling and measuring all the trees of the whole-stand plots, including suppressed trees, was rather time-consuming. Therefore, the competition part (chapter II) included only five such plots, although more plots would have represented better the different forest stand structures at low elevations.

**Potential for future research**

In this section, the potential of extending and broadening the multi-scale approach of this thesis is examined. I highlight some research gaps and some of the most interesting research questions, which have emerged from this thesis and are open for future research. Again, this section will refer to the description of the three main parts in the section above and to Figure 1.

*Upscaling in time:* Along with a changing climate regime over the long-term, changes in the growth response to climate (chapter I) can be expected. By means of moving response functions (Biondi & Waikul 2004), such changes can be evaluated over time. For this kind of analysis, the sampling should aim for long tree-ring chronologies, including trees of different ages and social status.

Similarly, when modelling forest succession (chapter III), climate changes were not simulated, although they are assumed to accelerate pine decline (cf. chapter I and II). Climatic changes could be evaluated by applying different climate scenarios. However, climate change effects have to be treated with much care, because ecological processes may change with changing conditions (e.g. Penuelas & Filella 2001, Walther 2004). An estimation of forest response to climate change has to deal with many problems (Loehle & LeBlanc 1996, Hanson
& Weltzin 2000), particularly when studying managed forests. Among others, the fire frequency is most likely to increase in a warming climate, and thus would also need to be considered when modelling forest succession at xeric sites (cf. Schumacher et al. 2004).

**Upscaling in space:** Because even at low elevations in Valais conditions are likely to differ from the sites studied here, the autecological analyses (chapter I) should be extended to different sites where Scots pine and pubescent oak occur. As shown in the patterns of the response functions, differences in soil and climatic factors will, to some degree, affect the radial growth of Scots pine and pubescent oak. This will also have an impact on the local competitive behaviour of the two species (chapter II). For a more general autecological basis, the sampling should be expanded into the area of pure pubescent oak and pure Scots pine stands, and to regions with older pubescent oak forests.

Concerning the competition part (chapter II), additional insights into the differences between the life history strategies of Scots pine and pubescent oak could be gained by investigating additional forest stands with various stand densities and species compositions along both an ecological and a successional gradient.

**Downscaling in time:** For an improved understanding of the climatological growth limits of Scots pine and pubescent oak in Valais, growth reactions to drought deserve to be studied on the wood anatomical level and with a higher than annual resolution, e.g. by using the pinning method (Wolter 1968, Schmitt et al. 2000). This technique provides a tool to relate cell formation and production to the exact time in the year. Thus, it allows for the study of intra-annual processes of cell growth such as cell differentiation, lignification and the development of growth over the growing period in relation to prevailing climatic conditions.

**Downscaling in space:** Although the modelling part included a forest-history based land-use scenario (chapter III), historical forest-use was not directly studied on the plot to compare with competitive interactions (chapter II). However, interdisciplinary case studies that combine historical and ecological methods may be valuable as a way of explaining the competitive patterns in tree growth in more detail. From a long-term perspective, historical land-use practices may even have led to the degradation of the soils in the forests studied here. Therefore, future changes in topsoil depth and nutrient availability are likely to occur and will contribute to determining the trajectories of future forest succession (chapter III).
the stand level, forest modelling will provide a tool to further evaluate the effects of different land-use scenarios on past and future forest development.

The retrospective dynamic competition index developed in chapter II was successfully related to parameters of aboveground competition, such as crown proportion and the proportion of dead branches. However, from the main results of this thesis, the growth of individual trees is also likely to be linked to competition for moisture. In particular, root volume and structure can be expected to play a major role in belowground competition and therefore deserve further investigation. In this way, the results of the dynamic competition index could be examined considering both above- and belowground parameters.

*Implicit upscaling in the model:* In forest gap models such as ForClim, usually implicit upscaling is performed to integrate species-specific growth (Bugmann et al. 2000), including drought response and the reaction to competition. In contrast, by means of dendroecological analyses explicit downscaling is often performed: Within this thesis, I derived physiological parameters from tree-rings and individual competitive patterns from the radial growth of neighbouring trees. The main conclusion from the latter approach is that suppressed trees are usually poorly represented in forest gap models, i.e. the trees either grow reasonably well, or they die. Therefore, a more realistic and more accurate mortality function would be useful in improving the model with respect to trees with slow growth (Bigler & Bugmann 2003). This will also enable a study of the influence of suppressed trees on forest dynamics. Moreover, modelling diameter growth based on tree-ring data may also result in a more realistic simulation of stand structure.

*Competition between Scots pine and pubescent oak as a driver for stand dynamics in Valais – new insights*

This thesis provides a scientific basis for estimating how differences in the life history strategies and the competitive ability of Scots pine and pubescent oak influence species composition and stand dynamics at xeric low-elevated sites in Valais. The results of the four chapters correspond to each other in many ways. Although each of the chapters addressed different questions at different scales in time and space (Fig. 1), they provide the crucial puzzle pieces for answering the overall research questions that are underlying this thesis:

- At these rather xeric sites, moisture availability was found to play a major role for the growth of both species. This was demonstrated by the high variance explained by climate
in the response functions (chapter I) and by the limitation of cell production in drought years (chapter IV). Moreover, pubescent oak was found to react more sensitively to changes in moisture availability than the coniferous Scots pine, which was much more dependent on prior growth (chapters I and IV). Also, the adaptation to drought turned out to be an important factor for the competition regime between the two species (chapters II and III). Using response functions, the sub-regional climate and soil conditions were found to be affecting the growth patterns much more strongly than the altitudinal site gradient (chapter I). This can probably be explained by the fact that in Valais, moisture availability changes only slightly with altitude, at least at elevations below 2000 m a.s.l. (cf. Lingg 1986).

- A changing climate, characterised by increasing summer drought due to increasing temperatures, will probably affect Scots pine more strongly than pubescent oak. Pubescent oak will certainly benefit if the climate changes towards more Mediterranean conditions (e.g. by changes in the seasonality of moisture availability, cf. Chapter I, Fig. 2), whereas pine is favoured in a continental climate (cf. Brzeziecki et al. 1995).

- Because the spread of pubescent oak to higher elevations can be assumed to be limited mainly by the frost tolerance of the saplings, increasing winter temperatures may favour the establishment of oak saplings at higher elevations in analogy to the upward shift of pine mistletoes (Dobbertin et al. 2005). However, for a comparison of the current upper limit of pubescent oak with the limit that was suggested by Burnand in 1976 (at 1200 m a.s.l.), the influence of low temperatures on the establishment of oaks needs to be evaluated in more detail. Temperature measurements on the 15 sampling plots used in chapter I showed that the altitudinal gradient in daily mean temperature from April to November 2003 is marginal (cf. Appendix 2). These values were recorded for altitudinal gradients of less than 400 m in altitude and at elevations below 1200 m a.s.l.

- With the analyses presented here, I was able to reveal the impact of increasing competitive pressure on the growth of individual Scots pine trees (chapter II). Recently, some of these trees have shown a decrease in their competitive ability, which is correlated with the proportion of dead branches, and therefore indicates increasing competition for light due to natural succession.

- Overall, historical land-use has considerably altered forest development in Valais. Simulating grazing effects on forest dynamics in Valais with the forest gap model ForClim (chapter III) was valuable as a way to detect then possible influences of past forest management on current forest structures. In this sense, the results of this thesis
agree with Silvertown & Charlesworth (2001), who stated that demonstrating mathematically whether a mechanism is operating can be “as important as field data to deciding what is really going on”. Furthermore, as Pacala (1997) asserts that modelling allows the testing of “hypotheses relevant to mechanisms explaining successional diversity that could not have been tested otherwise, given the scope of the temporal and spatial scales involved”.

- Many factors have the potential to contribute to pine decline in Valais. In contrast, at present, no particular factor is thought to be leading to high mortality rates of pubescent oak. However, an increasing abundance of pubescent oak may, in the longer term, lead to higher pathogen populations that are specialised on oak species.

- The scheme in Fig. 2 summarises potential trajectories of succession of forest stands in Valais that are emerging from the present work.

![Diagram](image-url)

**Fig. 2.** Theoretical scheme of forest succession at low elevations in Valais: The early stage of succession is occupied by pioneer stands with Scots pine (1). During succession, light availability decreases and later successional species such as pubescent oak become more abundant. Scots pine shows increased mortality rates due to less favourable light conditions (2). In the long-term, decreasing light and increasing pathogen abundances may partly lead to pure oak forest stands as a late successional stage (3). Small-scale disturbances, such as falling rocks and forest management, allow for the establishment of Scots pine saplings besides young and old pubescent oak trees (4). Large-scale disturbances (e.g. windthrow, fire) will again benefit the
establishment of pure pioneer stands with Scots pine \((2 \rightarrow 1, 3 \rightarrow 1, 4 \rightarrow 1)\). Browsing acts as a factor that is able to inhibit the establishment of pubescent oak, which will also result in Scots pine stands \((4 \rightarrow 1)\). At extremely dry sites, light availability may play a minor role compared to moisture availability. Therefore, Scots pine and pubescent oak may form mixed stands that are characterised by small tree heights and very low tree densities \((5)\).

**Implications for forest management and conservation**

From a practical point of view, forest management and conservation are essential to maintain particular forest functions in Valais, such as protection against natural hazards, species diversity and a characteristic landscape. In relation to current and future changes in species composition of the low-elevation forests, the following conclusions for forest management and conservation can be drawn from this thesis:

The competitive ability of some Scots pine trees as derived from radial growth was found to be reduced in mixed forests. In contrast, some pubescent oak trees showed increasing competitive strength. Without a reduction of oak stem density, the growth of Scots pines in these forests will therefore probably decrease further, and mortality is likely to increase. Thus, without forest management, Scots pine will at least partly be replaced by pubescent oak in these stands. To encourage the growth of Scots pine at places where Scots pine forests should be conserved for a particular reason, such as species conservation, foresters may therefore have to reduce total stand density to a lower level leading to a higher light availability in the crown area.

With the modelling part of this thesis, I could show that simulated forest succession was strongly dependent on the establishment rates. In Valais, the monitoring of establishing saplings of Scots pine and pubescent oak should therefore be intensified for a better understanding of the ecological factors that facilitate sufficient establishment rates. In particular, these observations should emphasise the availability and dispersal vectors of oak acorns and the limits of establishment given by low temperatures at higher altitudes and drought at extremely dry sites. For Scots pine, important factors for the establishment include seed production and quality as well as optimal conditions for germination and growth, i.e. enough light, bare soil and sufficient water availability. Consequently, improving the conditions for Scots pine or pubescent oak establishment by sowing or by providing light and bare soil will have an impact on the species composition in the future.
Furthermore, an exchange of forest management strategies with forestry partners from other inner-Alpine dry valleys where similar processes have been reported, such as the Vintschgau, the Aosta and the Inn valley, will certainly help to diversify the “forest action plan” for low-elevation forests in Valais.

**References**


Appendix I: Tree-ring chronologies

Standard and residual tree-ring chronologies provided a basis for calculating the response functions in Chapter I. Here, standardised mean chronologies for the fifteen sites sampled are shown.

Figure 1. Standard mean chronologies for all sites, for Scots pine (top) pubescent oak (bottom). They were used in Chapter I. Note: response function analysis was done for the period 1950-2001.
Appendix II: Temperature from April to October 2003

In 2003, temperatures were measured in four-hour intervals during the vegetation period (April to October) using three I-Buttons on each of the fifteen sampling plots (cf. Chapter I). Shown are daily mean temperatures. Despite the altitudinal gradient, mean temperatures run rather similar. These data were used for the interpretation of the response functions in Chapter I.

![Figure 2. Daily mean temperature measured from April to October 2003 on fifteen sampling plots situated at different elevations in Valais. The plots are described in Chapter I of this thesis.](image)
Appendix III: Spatial distribution of the trees

These figures provide more detailed information on the data used in Chapter II. Two examples are given for the distribution of the single trees on the five whole-stand sampling plots of 12 m in radius.

Figure 3. Spatial distribution of single trees on two sampling plots at Eschwald (top: esa, bottom: esb). Trees inside the outer circle of 9.5 m radius were treated in the competition analysis.
Appendix IV: Competitive patterns of individual trees

This Appendix includes the individual trees’ retrospective dynamic competition indices over time, which were calculated as a basis for Chapter II. Each diagrams shows the curves of one of the five analysed plots. Also, average curves of competitive dynamics are drawn for Scots pine and pubescent oak.

Fig. 4. Individual dynamic competitive patterns. Shown are the curves of the retrospective dynamic competition index for single pubescent oak (grey) and Scots pine (black) trees on two sampling plots (esa (top); esb) and the average of all single Scots pine and pubescent oak trees (thick lines).
Fig. 5. Individual dynamic competitive patterns. Shown are the curves of the retrospective dynamic competition index for single pubescent oak (grey) and Scots pine (black) trees on three sampling plots (egb; saa, sab; from top to bottom) and the average of all single Scots pine and pubescent oak trees (thick lines).
Appendix V: Stand structures

More detailed information regarding Chapter III is given in this Appendix. The basal area and stem number distribution assigned to classes of 5 cm in dbh (diameter at breast height) are shown for the eight plots used for achieving the empirical data to compare with the simulated data.

Figure 6. Basal area distribution of eight whole-stand plots of 12 in radius that were used in Chapter III. Basal area is shown for Scots pine (grey) and pubescent oak (dark grey) and for dbh-classes of 5 cm.
Figure 7. Stem number distribution of eight whole-stand plots of 12 in radius that were used in Chapter III. Stem numbers are shown for Scots pine (grey) and pubescent oak (dark grey) and for dbh-classes of 5 cm.
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Curriculum vitae

Pascale Anja Weber

Born August 12th, 1972 in Zürich, Switzerland
Citizen of Zürich (ZH), Switzerland

1992 Matura Type B, Kantonsschule St. Gallen, Switzerland

1992 – 1998 Studies in Environmental Sciences at the Swiss Federal Institute of Technology (ETH)

1998 Diploma thesis (Dipl. Umwelt-Natw. ETH): „Ökologische Bedeutung von Niederwäldern. Potentialabschätzung für den ehemaligen Niederwald Fluh in Untersiggenthal (AG)“, under the supervision of Prof. Dr. K. C. Ewald (Nature and Landscape Conservation, ETH Zurich) and Dr. T. A. Walter (formerly ETH, currently FAL Reckenholz)

1996 Practical work for five months at the Forestry Division of Canton Schwyz

1999 Practical work with GIS for six months at the Forestry Division of Canton Aargau

1999 – 2001 Research assistant in Wood Sciences at the Forestry Department of ETH Zurich

2001 – 2005 Ph.D. thesis at the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) and at the Swiss Federal Institute of Technology (ETH): „Inter- and intraspecific competition in mixed Quercus pubescens and Pinus sylvestris stands - Modelling future dynamics based on tree-ring analysis“, under the supervision of Prof. Dr. H. Bugmann (Forest ecology, ETH Zurich), Dr. A. Rigling (WSL, Birmensdorf) and PD Dr. F. Kienast (WSL, Birmensdorf)