THÈSE

Tree regeneration and growth in wood pastures: patterns and processes

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IMPRIMATUR POUR LA THESE

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Ce qui ne nous tue pas, nous rend plus fort.

Friedrich Nietzsche

dans *Ainsi parlait Zarathoustra*

Abstract

Keywords: multi-scale approach, descriptive study, Swiss Jura Mountains, Norway spruce, *Picea abies*, regeneration niche, competition, cattle browsing, suppressed growth, compensatory growth, plant community, unpalatable plant species, associational resistance, nurse structure, self-enhancing feedback mechanism, pasture woodland, shifting mosaic.

Tree regeneration and growth are major processes shaping silvopastoral ecosystems, driving the coexistence of closed forest patches and open grasslands within a dynamical mosaic over space and time. A better understanding of these processes and resulting patterns are crucial both for sustainable landscape management including biodiversity conservation. This thesis focuses on *Picea abies*-dominated wood pastures of the Swiss Jura Mountains, on established tree saplings (>1 year) up to 1.5 meters height, using field descriptive methods and correlation analyses at four different scales: 1 dm^2, 1 m^2, 4 m^2 and 25 m^2, in order to investigate four hypotheses: (i) established tree saplings were spatially associated with nurse structures such as shrubs, tree stumps, rock outcrops and unpalatable plants, as predicted by the associational resistance hypothesis; (ii) tree recruitment is dependent on the local plant community even after accounting for abiotic environment and unpalatable species; (iii) positive and negative associations between *Picea* saplings and neighbouring plant species depend on scale; and (iv) neighbouring trees can play the role of facilitative structures despite increased competition.

Tree sapling surveys, records of abiotic environmental factors (microtopography, soil, light), vegetation relevés and mapping of canopy trees were achieved in two study sites: La Sagne (NE) and Marchairuz (VD). In addition, comparative growth analyses were done between browsed and non-browsed *Picea* trees, based on an original none-invasive method using branch age and size to establish tree growth curves.

Our results showed that the few small trees above the herbaceous layer represented the small emerging part of a complex story taking place in the shade of the herbs. In particular, *Picea* saplings up to 40 cm were positively associated at the scale of 4 m^2 with nurse structures such as rock outcrops, stumps, shrubs and unpalatable plant species, suggesting that those structures constitute safe sites for tree recruitment. Furthermore in the herbaceous layer, far from shrubs and neighbouring trees, small *Picea* saplings were associated with specific assemblages of plant species at the scale of 1 m^2, related to specific growth conditions in relation with competition for resources and attractiveness for herbivores. At the finer scale of 1 dm^2, the species-specific nature of the association vanished in favour of an association with species morphological traits, possibly closer to the underlying mechanism influencing sapling growth and survival. At a broader scale (resolution: 25 m^2), tree saplings up to 1.5 m height appeared to be associated with shrubs, and when those were absent, a positive association occurred with the canopy tree cover, revealing a possible self-enhancing effect of higher neighbouring *Picea abies* against the impact of cattle, despite conditions of potentially high intraspecific competition.

On *Picea* saplings of increasing size, the constraints were changing. Its survival required a succession of adaptive strategies in response to changing constraints. *Picea* saplings displayed a height-threshold at 1.5 m, below which both height and lateral growths were reduced whereas branchiness and wood/leaf ratio increased, as a possible adaptative response against browsing pressure. Above 1.5 m, growth suppression was released and compensatory growth was observed up to 2.3 m height.

In conclusion, if *Picea* saplings do have enough time to survive despite their low growth rate and large biomass ratio invested into leaves, they reinforce their below-ground position and develop an adaptive shape which protects their shoots against browsing. The survival as juveniles and resistance to browsing allow them to become such a dominant species in the wood pastures of the Jura Mountains. Our study contributed in better defining the regeneration niche of *Picea abies* in wood pastures of the Swiss Jura Mountains.

Résumé

Titre: Régénération et croissance des arbres en pâturage boisé : structures et processus écologiques

Mots-clés: approche multi-échelle, étude descriptive, Jura suisse, épicéa, *Picea abies*, niche de régénération, compétition, abroutissement par le bétail, croissance contrainte, croissance de compensation, communauté végétale, plantes non-appétantes, structure protectrice, auto-facilitation, pâturage boisé, mosaïque, dynamique spatio-temporelle.

La régénération et la croissance des arbres sont des processus écologiques majeurs déterminant la coexistence des éléments boisés et des herbages dans les écosystèmes sylvopastoraux selon une mosaïque dynamique dans l'espace et le temps. Cette étude s'intéresse en particulier aux plantules d'épicéa (*Picea abies* (L.) Karst) âgées de plus d'un an mais inférieures en taille à 1.5 m, dans les pâturages boisés du Jura suisse. A l'aide de méthodes descriptives mises en œuvre sur le terrain à quatre résolutions spatiales différentes (1 dm^2, 1 m^2, 4 m^2 et 25 m^2), quatre hypothèses principales sont testées: (i) les plantules sont installées de préférence au voisinage de structures protectrices telles que des buissons, des souches, des affleurements rocheux et des plantes non-appétantes pour le bétail; (ii) le potentiel de régénération dépend des communautés végétales environnantes, même si l'on retire l'effet des conditions abiotiques et du voisinage d'espèces non-appétantes; (iii) les associations positives et négatives dépendent de la résolution spatiale considérée; et (iv) le voisinage d'autres arbres peut jouer le rôle de structure protectrice malgré des conditions de compétition accrûes.

Sur la base d'inventaires de plantules, de mesures environnementales (microtopographie, sol, lumière), de relevés de végétation et d'une cartographie des arbres dans les deux sites d'étude établis au Marchairuz (VD) et à La Sagne (NE), il ressort à l'échelle de 4 m^2 que les plantules d'épicéas d'une taille inférieure à 40 cm sont positivement associées aux structures protectrices telles que des affleurements rocheux, des souches, des buissons et des plantes non-appétantes, ces microsites leur étant favorables. De plus, en l'absence de buissons, les plantules d'épicéas sont liées à un assemblage spécifique d'espèces à l'échelle du m^2, en relation avec leur attractivité pour le bétail et leur faculté compétitive. A l'échelle du dm^2, l'identité des espèces joue un rôle moins déterminant que les traits morphologiques des plantes, qui constituent à cette échelle des descripteurs de la végétation probablement plus proches des mécanismes sous-jacents. A l'échelle la plus vaste (25 m^2), il apparaît que les petits arbres jusqu'à 1.5 m sont positivement associés avec les buissons, et lorsque ceux-ci sont absents, avec d'autres arbres du couvert forestier, révélant un effet protecteur contre l'impact du bétail, ceci en dépit des conditions accrûes de compétition intraspécifique.

Les contraintes affectant des plantules d’épicéa changent au fur et à mesure de leur croissance. Leur survie nécessite ainsi une succession de stratégies adaptatives en réponse aux contraintes environnementales changeantes. Les résultats obtenus à l’aide d’une méthode non destructive originale mise au point pour établir des courbes de croissance sur la base d’une analyse des branches révèlent ainsi un seuil important à une hauteur de 1.5 m. Pour les épicéas inférieurs à 1.5 m, la croissance latérale et verticale est réduite, tandis que le degré de ramification des branches et la proportion entre le bois et les feuilles produits annuellement augmentent, constituant une réponse adaptative contre la pression d’abroutissement. Au-delà, la croissance n’est plus contrainte et une surcompensation est même observée jusqu’à une hauteur de 2.3 m.

En conclusion, si l’épicéa bénéficie d’un temps suffisant pour survivre en dépit de sa croissance lente et de la proportion importante de biomasse allouée dans les feuilles, il devient en mesure de renforcer sa position par un enracinement important, tout en développant une forme de croissance adaptée pour résister à la pression d’abroutissement sur ses jeunes pousses. Ceci permet ainsi à cette espèce à croissance lente le succès qu’on lui connaît dans les pâturages boisés du Jura. Ce travail contribue ainsi à une meilleure définition de la niche de régénération de l’épicéa en contexte pâturé.

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INTRODUCTION

Wood pastures

Wood pastures are traditional semi-natural ecosystems formed by the combination of extensive pasturing and logging activities, formerly very abundant in Europe. They comprise vegetation types that range from open grasslands to closed forests, including pastures with scattered or clumped trees and shrub thickets (Gillet & Gallandat 1996a, Gillet & Gallandat 1996b, Vera 2000). Across Europe, the surface of these silvo-pastoral ecosystems declined dramatically during the last century, mainly because of local intensification or extensification of agricultural practices. Still abundant in the Swiss Jura Mountains where they represent the most frequent landscape type at an elevation between 800 m and 1400 m a.s.l., wood pastures occupy a wide range of topographical positions, from flat to steep slopes of varying aspect, with soils varying from bare limestone outcrops to deep fertile silty soils (Gallandat et al. 1995, Havlicek et al. 1998).

Cattle herds in wood pastures are mainly composed of heifers and dairy cows, grazing over the summer period (June to September) only, because of the typical climate of temperate mountainous regions (mean annual temperature: 7°C; mean annual rainfall: 1600 mm at 1200 m a.s.l.). Two grazing systems generally occur (Gillet & Gallandat 1996a): (i) free ranging; the animals graze the entire summer season in a single wide-ranging pasture; (ii) grazing rotation; the pastures are subdivided into paddocks and animals are grazing successively in each one, according to a variable rotation period which depends on the available forage. In both grazing systems, shrubs and unpalatable weeds are partially removed by the farmers in order to prevent loss of grazing area.

The forest management in wood pastures remains extensive and is generally of low economical value. Mainly dying or affected trees are logged, and the stumps are usually left on place. Where natural tree regeneration fails, new saplings may be planted and fenced for their protection against cattle, but natural tree regeneration is highly predominant (Gallandat et al. 1995). One conifer species (*Picea abies* L. Karst) and two deciduous tree species (*Acer pseudoplatanus* L. and *Fagus sylvatica* L.) are dominant, *Picea abie*s being the most abundant species, probably beneficiary from forestry and agricultural land use over the last centuries (Gallandat et al. 1995).

Wood pastures are both organisationally and functionally complex ecosystems, in which cattle play a predominant role. The activity of large herbivores drives the vegetation dynamics of wood pastures (Olff & Ritchie 1998, Gillet et al. 2002, Bakker et al. 2004, Smit et al. 2006), affecting vegetation by herbage removal, tree-shrub browsing, trampling, and dung-urine deposition (Schlapfer et al. 1998, Bakker & Olff 2003, Rook et al. 2004). Such local disturbances create a highly heterogeneous and fluctuating environment, which results in local changes in the vegetation composition and generates complex patterns at several spatio-temporal scales (Kohler et al. 2004, 2006a, Kohler et al. 2006b). The mosaic of trees, shrubs and open grasslands offers various microclimates (Gillet et al. 1999), and both high soil variability and spatial heterogeneity contribute to a wide range of ecological conditions within short distances (Havlicek et al. 1998). The interplay of this wide range of ecological conditions and processes results in a particularly high level of plant diversity over time and space, even at fine scale (Dufour et al. 2006). A better understanding of vegetation patterns and underlying processes is therefore of highest importance for long term conservation of those threatened man-made landscapes, through efficient management schemes, based on traditional scientific observations and complementary experimentations.

Tree regeneration

Natural tree regeneration is one of the major ecological processes driving silvo-pastoral ecosystems (Buttler et al. submitted). The maintenance of the unstable equilibrium between open grasslands and closed forests directly depends on the amount and the spatial distribution of regenerating trees. The latter will determine the location and the stand density of the coming tree cohort, as well as the landscape aspect of wood pastures. In turn, through a feedback effect, adult trees will influence cattle habitat use, and therefore also the progression towards an intensification or extensification of pastoral land use.

Regenerating trees have to be successful in a variety of life stages, meeting the specific hazards of each vegetation layer they penetrate (Harper 1977). The establishment stage of a tree species comprises different sequential phases: (i) the seed phase; (ii) the seedling phase which comprises the first year after germination; and (iii) the sapling phase. Each phase is driven by several ecological processes and mechanisms, in a context of numerous and changing hazards.

Because most tree species do not form seed banks (Burrows 1990, Milberg 1995, Wijdeven & Kuzee 2000), new sites need to be colonized by seeds whereby many species rely on wind or animals for seed dispersal (Willson 1993). If the seeds survive to desiccation, fungi, and numerous seed predators (Pigott 1985, Davidson 1993, Meiners & Stiles 1997, Ostfeld et al. 1997, Wenny 2000), they can germinate under suitable biotic and abiotic conditions. After germination, during the seedling and sapling phases, young trees have to cope with several abiotic factors like microtopography, microclimate and resource availability (Kuuluvainen 1994, Canham et al. 1996, Tripler et al. 2005, Messaoud & Houle 2006). In addition, biotic factors due to neighbouring plant species, herbivores interactions and below-ground micro-organisms communities will have strong influence on sapling growth and survival (Andre et al. 1987, Rousset & Lepart 2000, Gorchov & Trisel 2003, Pagès & Michalet 2003, Dolezal et al. 2004, Vandenberghe et al. 2006). Finally, the framework of the soil, humus type, litter and possible rotten logs or stumps, and their properties will determine further biotic and abiotic conditions driving tree establishment (Bernier et al. 1993, Facelli 1994, Jaderlund et al. 1996, Szewczyk & Szwagrzyk 1996, Ponge et al. 1998, Nakagawa et al. 2003, Simard et al. 2003).

Facilitation *versus* competition

Facilitation, the process whereby a plant species is more likely to get established in the presence of a second species (Allaby 1998) was recently identified as being prominent in plant ecology (Callaway 1995, Lortie et al. 2004, Tirado & Pugnaire 2005, Cheng et al. 2006). The potential for palatable species to escape herbivore pressure by associating with unpalatable plant species has been described as associational resistance, associational refuge or associational defence (Atsatt & Odowd 1976, Milchunas & Noy-Meir 2002), and proposed to play an important role for tree establishment in grazed grasslands.

The positive effects of facilitation on sapling survival are often balanced by competition (Callaway & Walker 1997, Holmgren et al. 1997, Choler et al. 2001, Arsenault & Owen-Smith 2002, Miriti 2006), the net effect being finally the determinant one for the constrained/facilitated species (Berkowitz et al. 1995, Maestre et al. 2003). The alternation of associational resistance and competition was proposed by Olff et al. (1999) to be a key process in the vegetation dynamics of temperate wood pastures, leading to cyclic shifts in vegetation mosaics. Observations of spatial association patterns support this theory (Rousset & Lepart 1999, 2000, Bakker et al. 2004) but studies addressing the mechanisms which underlie such patterns of spatial association and their influence on long-term remain scarce.

In a three part system, when the different pairs of species compete for different resources or have different mechanisms for acquiring these resources, an indirect positive effect may be observed, known as indirect facilitation (Levine 1999). Several modelling and experimental studies investigated it in a wide range of ecosystems (e.g., Stone & Roberts 1991, Miller 1994, Pagès & Michalet 2003). As illustration of this concept in forest communities, if herbaceous species compete with tree seedlings for nutrients, whereas the same herbaceous species and tree seedlings are under the competition pressure of adult trees for another resource such as light, adult trees may indirectly facilitate tree seedlings in affecting negatively the herbaceous species (Levine 1999). This highlights the role of indirect interactions in addition to direct facilitation and competition in the structure of plant communities (Miller 1994, Callaway & Walker 1997).

Picea abies - a keystone species?

Norway spruce (*Picea abies* L. Karst) is the most dominant tree species in wood pastures of the Swiss Jura Mountains (Gallandat et al. 1995). It has been hypothesized in the framework of the NCCR-PS6 project, to which this thesis belongs to, '*Pattern and long-term changes in pasture-woodlands: complex plant-herbivore interactions in a traditional type of agro-forestry*' to be a keystone species of silvo-pastoral ecosystems, due to its dominance and ability to outcompete other species.

From species frequency distributions often characterized by a few abundant species and many rare ones, and from the analyses of food webs and interaction strengths, it is obvious that not all species within a community have equal functional roles (Menge et al. 1994, Berlow 1999, Goldberg et al. 1999, Magurran 2005). In this context, Paine (1966, 1980) formalized the component of this inequality with the definition of a keystone species, which is a species whose functional role is disproportionately exceeds its relative abundance. Difficulties in identifying such species contributed to a partial recognition of this concept (e.g., Power et al. 1996), and other authors even suggested abandoning it (e.g., Hurlbert 1997).

In the wood pastures of our study, both the high abundance and dominance of *Picea abies* suggest that this conifer tree species rather corresponds to a foundation or an umbrella species than a keystone species. An umbrella species is a target species in conservation biology (Caro & O'Doherty 1999, Roberge & Angelstam 2004), supposed to be largely representative of an entire species community of a given ecosystem. Hence, the protection of a viable umbrella species population is assumed to result in the protection of populations of other sympatric members of the same guild (Berger 1997), biota at lower trophic levels or appreciable parts of the ecosystem (Launer & Murphy 1994). Moreover, foundation species were defined by Bruno & Bertness (2001) as species providing habitats for other species and, by this mean, being determinant for the overall species diversity. Bruno et al. (2003) suggested that forests in particular may be habitats based on foundation species. In the current view, many foundation species are considered as competitive dominants, excluding other potential primary space holders (Paine 1966, Dayton 1971, Power et al. 1996). Whatever the most appropriate term characterizing *Picea abies* in wood pastures is, this species certainly has significant nontrophic impacts on the wood pasture ecosystem structure, function, and biodiversity, justifying the main focus of the present study on its regeneration and growth.

Outline of this thesis

The aim of this thesis is to get insight into patterns and underlying processes of tree regeneration and growth in the *Picea abies*-dominated wood pastures of the Swiss Jura Mountains. The original TRUFE concept of this thesis was to consider the relations between *Picea abies* and its environment as a whole, from the initial regeneration phases to a tree influencing its environment through a feedback effect (Figure 1). During the first life stages, the tree sapling is mostly under the constraint of its environment, which influences establishment potential and survival chances. Once above a given threshold in size and time, the tree will get free of its environment, and become a increasing constraint on the surrounding environment, in particular on the components of the environment which were previously determinant to its establishment. We focus particularly on the vegetation and microsite components of the sapling environment, in relation with the influence of cattle (Figure 1).

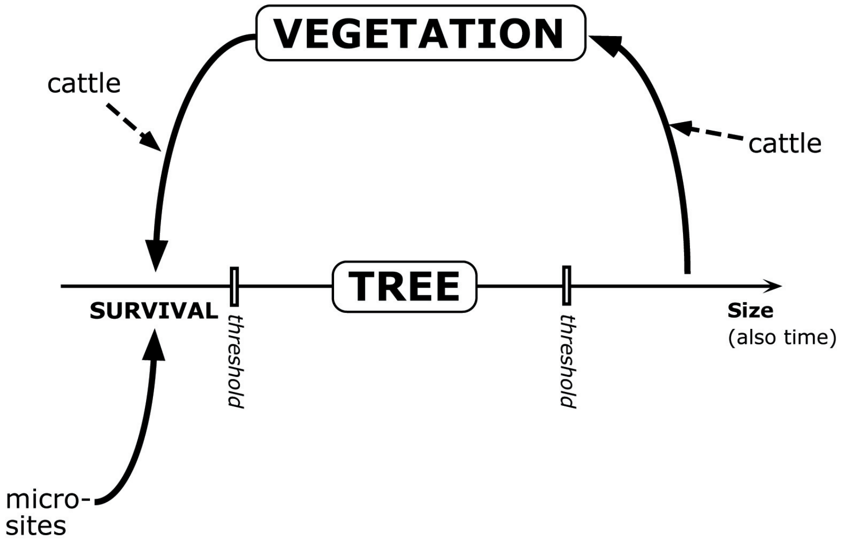

Figure 1: The TRUFE concept of Tree Regeneration and Understorey Feedback effect. During the first life stages, the Picea sapling survives under the constraints of microsite conditions and the surrounding vegetation partly mediated by the activity of cattle. Above a height (and time) threshold, the growing tree gets mainly free from these constraining factors and becomes constraining in particular on the surrounding vegetation through the understorey feedback effect.

The positive influence of the surrounding vegetation on the tree sapling can be decomposed into two facilitative effects (Figure 2): (i) facilitation by specific herbaceous species, with functionally well-defined properties such as unpalatability or toxicity, and (ii) vegetation properties resulting from the species assemblage. In addition, environmental abiotic factors such as microtopography, light and soil conditions may contribute positively to the establishment and growth of *Picea abies* saplings. Initially struggling for survival, the growing *Picea* tree will become more and more influent until it gets a dominant constituent of the environment in wood pastures (Figure 2).

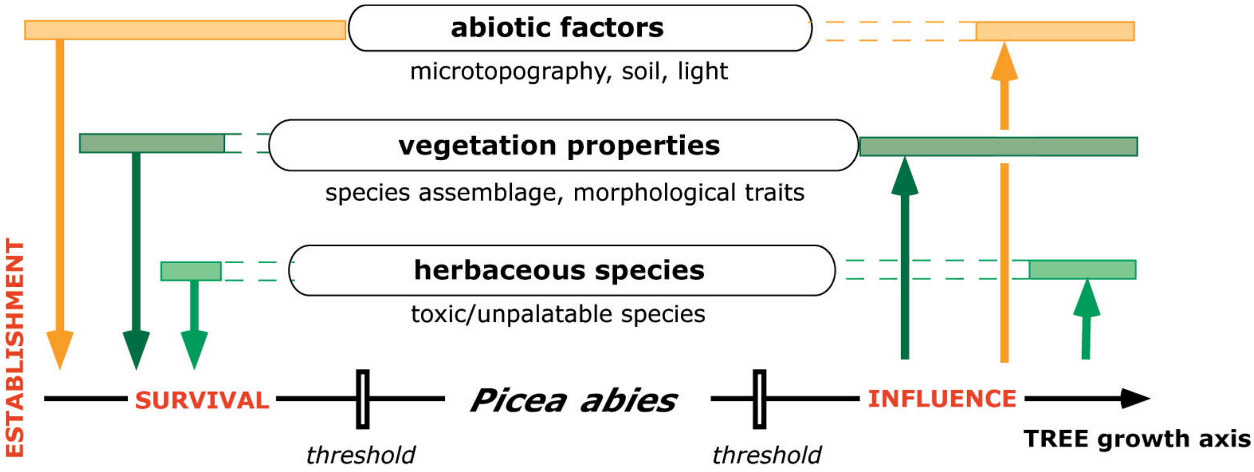

Figure 2: Positive effects and feedback along the life stages of Picea abies in wood pastures. The positive effect of the surrounding vegetation can be subdivided into facilitation by specific herbaceous species such as toxic or unpalatable species, and facilitation by vegetation properties due to species assemblage and morphological traits. In addition, facilitation by abiotic factors such as microtopography, light and soil conditions will influence tree establishment and early survival. Once above a given size, the Picea tree will influence in particular these environmental conditions which have allowed its establishment and survival.

From the ambitious objective of a better understanding of each aspect of the TRUFE concept, I finally focussed my thesis mostly on tree recruitment in relation to microsites and surrounding vegetation (Chapters 1, 2 and 3). I then take brief outlooks on association patterns at the stand level (Chapter 4), on *Picea* growth responses under direct cattle influence (Chapter 5) and on the possible role of tree stumps as new initial conditions for tree recruitment in relation with shrub communities (Chapter 6).

The objective of the first study is to determine whether established tree saplings were spatially associated with specific nurse structures, such as shrubs, tree stumps, rock outcrops, overhanging tree branches and unpalatable plants, as predicted by the associational resistance hypothesis (Chapter 1).

In the second chapter, I explore whether local plant communities as a whole, rather than individual unpalatable species, enhance tree recruitment in wood pastures. In particular, I'm testing the following hypotheses: (i) at a given site and at a scale of 1 m^2, tree recruitment is dependent on the local plant community, independently of the effect of local environmental conditions and the presence of individual unpalatable species with facilitative effects; (ii) the balance between positive and negative interactions changes for a given species in relation to site conditions; (iii) different species could play the same facilitative role for tree saplings (Chapter 2).

The question of scale remaining mostly untreated in studies on facilitative interactions, we then test whether positive and negative associations between saplings of *Picea abies* and neighbouring plant species vary across different scales (Chapter 3).

Focussing more generally on other woody species in the *Picea* neighbourhood such as shrubs and canopy trees, I explore the following hypotheses: (i) presence and abundance of shrubs enhance the recruitment of tree species under grazed conditions; (ii) neighbouring trees can play the role of facilitative structures for tree saplings, in particular when no other nurse structure offers protection against cattle browsing. Testing these hypotheses will allow answering the general question of what the current spatial pattern of trees can tell us about the major processes driving past and present tree recruitment and growth in the pasture woodland context (Chapter 4).

Mostly considered indirectly through the mediation of associational resistance, the direct effect of cattle browsing on *Picea abies* growth is investigated in the fifth part of my thesis. In particular, I will present a none-invasive method to study past apical growth of *Picea abies* trees, as well as some results and perspectives resulting from the description of growth patterns of browsed *Picea* trees in wood pastures (Chapter 5).

Finally, the perspective of a possible support for the shifting mosaic theory (Olff et al. 1999) will lead us to the sixth and last part of this thesis, where I briefly explore the positive association of tree stumps and *Picea* tree recruitment, a with the possible mediation effect of shrub species (Chapter 6).

CHAPTER 1

Safe sites for tree regeneration in wooded pastures: a case of associational resistance?

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Journal of Vegetation Science ***16****: 209 - 214.*

Abstract

Question: Are tree saplings in wooded pastures spatially associated with specific nurse structures or plants that facilitate tree sapling survival?

Location: Wooded pastures in the Jura Mountains of Switzerland.

Methods: In two sites, 73 km apart, we sampled a total of 294 plots of 4 m^2, systematically distributed on 1ha, and a) recorded number and height of all established *Picea abies* saplings (>1 year and up to 40 cm in height), and b) visually estimated cover of rocks, shrubs, tree stumps, overhanging tree branches and unpalatable plant species.

Results: Despite differences in site characteristics, we found overall positive effects of cover of unpalatable plants, rocky outcrops and tree stumps on the density of *Picea* saplings per plot. Plots with tree stumps and higher cover of rocky outcrops and unpalatable plants were more likely to contain *Picea* saplings.

Conclusions: Unpalatable plants, rocky outcrops and tree stumps seem to form safe sites for *Picea* saplings in this grazed system, improving their establishment and survival. Our findings support the idea that associational resistance drives the dynamics of wooded pastures, but experimental evidence for this hypothesis is still required.

Keywords: Facilitation, nurse plant, tree establishment, grazing, tree saplings, *Picea abies*

Nomenclature: Tutin et al (1964-1980).

Introduction

Spatial associations of tree saplings with other vascular plant species, often shrubs, are found in a wide range of ecosystems, such as savannas or grasslands (Rousset & Lepart 1999, 2000, 2002, Weltzin & McPherson 1999), woodlands (Chambers 2001, Kitzberger et al. 2000, Callaway 1992), old fields (Li & Wilson 1998, Meiners & Gorchov 1998), mountain shrub steppes and forests (Callaway et al. 1996), chaparral (Dunne & Parker 1999) and laurel forests (Arevalo & Fernandez-Palacios 2003). These associations often suggest nurse effects of the neighbouring plants, through direct or indirect contributions to the performance of the saplings by 1) providing shelter from extreme temperatures and high irradiance, 2) increasing water availability (water uplift, higher water infiltration rate and reduced evaporation), 3) improving nutrient availability, 4) offering physical support, 5) reducing soil compaction and erosion or 6) protecting from herbivores (Flores & Jurado 2003). Detecting spatial associations helps to understand dynamics of ecosystems (Castro et al. 2002).

Recent studies focussed on cattle-grazing ecosystems report spatial associations of tree saplings with grazing resistant plants which are often defended by physical or chemical mechanisms and therefore avoided by cattle (Rousset & Lepart 1999, Kuiters & Slim 2003, Bakker 2004). This suggests that close association with unpalatable plants can reduce herbivory on tree saplings, leading to a net positive result for the tree saplings. This process, also known as associational resistance or defence guilds (Atsatt & Odowd 1976) is proposed as a key process in the dynamics of grazed temperate woodlands leading to cyclic shifts in vegetation mosaics (shifting mosaic theory, Olff et al. 1999): unpalatable plants in open grassland facilitate other unattractive high forbs and shrubs, which facilitate trees, which outcompete in turn their original facilitators. Since undergrowth and hence tree regeneration underneath these trees is prevented, open grassland may reappear after the tree dies. Thus, the landscape remains a mosaic of grassland and forest patches. The cattle-driven cyclic shifts are seen as highly important for the maintenance of spatial and temporal variation in vegetation structure, leading to high biodiversity in extensively grazed ecosystems in temperate zones (Olff & Ritchie 1998).

Wooded pastures or pastured woodlands are traditional semi-natural ecosystems, combining extensive pasturing and logging with natural regeneration of grassland and woodland. Wooded pastures may find their origin in the Neolithic with the first farming activities of man (Pott & Hüppe 1991), but it has also been hypothesised that domesticated animals have taken over the role of their now-extinct ancestors (e.g., aurox, tarpan) in maintaining similar vegetation patterns (Vera 2000). Wooded pastures have declined drastically in Europe during the last few decades, mostly due to concentration of agricultural management, leading to local intensification and abandonment elsewhere (Gillet & Gallandat 1996, Pywell et al. 2002). Considerable areas of wooded pastures are still to be found in the Swiss Jura Mountains, at altitudes between 900 and 1400 metres (Gillet & Gallandat 1996). These species rich landscapes with high conservation values are presently highly threatened. The dynamics of these systems are yet little investigated and a better understanding is crucial for sustainable management and conservation purposes.

The objective of our study was to determine whether established tree saplings were spatially associated with potential nurse structures, such as shrubs, tree stumps, rock outcrops, overhanging tree branches and unpalatable plants, as predicted by the associational resistance hypothesis. A positive association is the prerequisite for associational resistance, the suggested key process in the dynamics of these wooded pastures, although it could be generated by other processes as well.

Methods

Study sites

This study was conducted in two wooded pastures, about 73 km apart, lying in the central part of the Jura Mountains in western Switzerland (Table 1). The climate is continental, with Atlantic influences bringing depressions from the West. Mean yearly temperature varies between 5 and 3° C for site 1 and 2 respectively. Although annual precipitation is between 1400 and 2000 mm (with peaks in summer) the soils are considered relatively dry because of the high permeability of the underlying calcareous layers (Gallandat et al. 1995). In combination with low winter temperature, this leads to a relatively short growing season of approximately four months. Every year, the ground is covered by snow during about 120 days between November and April.

The landscape is typically very heterogeneous with large geomorphological and geological variations. This influences vegetation pattern, with closed forest patches being mainly associated with rock outcrops and steep slopes, pastures and wooded pastures with flat surfaces or gentle slopes where the soils are more favourable for agriculture. Norway spruce (*Picea abies*) is the naturally dominant tree species, occurring as isolated individuals or in small groups in open grasslands. Other tree species, like maple (*Acer pseudoplatanus*), white fir (*Abies alba*) and beech (*Fagus sylvativa*), do occur in the surrounding ungrazed forests at relatively low frequencies, but are rarely found in the pastured areas.

Table 1: Characteristics of the study sites and pasturing conditions for the year 2002.

Site	1. La Sagne	2. Marchairuz
Coordinates	6°47' N, 47°3' E	6°12' N, 46°32'E
Size (ha)	400	102 (15[*1])
Altitude (m a.s.l.)[*2]	1150	1340
Slope (°)[*2]	16	15.7
Aspect	S	N
Grazing system	Free ranging	Four rotations
No. of grazing days	112	108 (40[*1])
No. of animals	369 cows, 15 horses	50 cows, 3 horses
Grazing period	mid-May - end Sept.	end May - end Sept.
Grazing intensity[*3]	50 LU days/ha	82 LU days/ha

[*1]Size selected park; [*2] Mean values; [*3]Estimated value;1 LU (livestock unit) = 600 kg body weight. Grazing intensity calculated as: (nr. LU * nr. grazing days) / total grazed area.

The mainly dry and calcareous grasslands are mostly of the *Mesobrometum* type, harbouring some of the most species-rich plant-communities of Central Europe (Pykala 2003, Schläpfer et al. 1998; Gallandat et al 1995, Vittoz 1998).

Two grazing systems are commonly applied: 'free-ranging' where animals spend the whole grazing season roaming freely through unpartitioned pastures, and 'rotation-grazing' where pastures are divided in parks and animals pass from one park to another according to a variable period of rotation (Gillet & Gallandat 1996). Cattle, sometimes mixed with horses, are generally brought up to the pastures in May and transported back at the end of September.

In each site we selected a representative surface with the constraint of having a tree cover ranging from 20 to 60%, dominated by *Picea abies* and with occurrence of young trees. Site 1 is situated in the Communal de la Sagne and is grazed by free ranging cattle. Site 2 is situated in Marchairuz (Pré-aux-Veaux), and belongs to the larger Parc jurassien vaudois. It is divided into roughly even sized parks, which are grazed in turns (rotation system); our selected park measured ca 15 ha. The herd grazes eight to ten days per park before passing to the next. Aside from occasional roe deer (*Capreolus capreolus*) and alpine hare (*Lepus timidus*) no other large vertebrate herbivores have been observed at our study sites.

Collecting data

All fieldwork was carried out between June and October 2002. At each study site we systematically laid out 150 plots of 4 m^2 on ten transect lines, with 15 plots per line, covering a total area of about 1ha. Lines were 10 m apart and plots along lines were 5 m apart. In each plot the number and height of *Picea abies* saplings (> 1 year old, up to 40 cm in height) were recorded and we visually estimated percentage cover of: (i) rocks (uncovered rocky outcrops), (ii) shrubs (woody shrub species > 40 cm tall), (iii) overhanging tree branches (lower than 150 cm), (iv) tree stumps and (v) unpalatable plant species (from an a-priori list) using Braun-Blanquet scale (Braun-Blanquet 1964). Cover scores (seven levels) were converted to percentage median values for statistical analyses. *Picea* seedlings emerging in the current year (< 1 year old) were not recorded since we would have measured effects of the 'nurse' structures on seed germination and emergence, rather than on establishment and survival. Saplings > 40 cm tall were not included since some of these were actually relatively old (ca > 50 years, unpubl.), but remained small due to constant browsing by cattle, and could have outcompeted their original facilitators.

The a-priori list of unpalatable species was derived from literature and personal observations (species left untouched by cattle after a grazing season), and mainly contained relatively large "obvious" unpalatable plant species, i.e. tall species with clear mechanical defences like spines and thorns or with well established toxic chemical compounds. These were *Cirsium acaule*, *Cirsium eriophorum*, *Carduus defloratus*, *Carlina acaulis* (mechanically defended), *Gentiana lutea*, *Veratrum album*, *Atropa bella-donna*, *Urtica dioica*, and *Ranunculus aconitifolium* (all chemically defended). We encountered the following shrub species: *Rosa canina*, *R. pendulina*, *Rubus idaeus*, *R. saxatilis*, *R. fructicosus*, *Ribes alpinus*, *Crataegus monogyna* (all physically defended), and *Juniperus communis* (both physically and chemically defended). These species were recorded as unpalatable when present as small individuals in the herb layer (single stemmed, < 40 cm), since we considered them not yet fully able to offer physical protection against cattle.

Data analyses

We compared the two sites for differences in sapling density, number of plots with tree saplings and percentage cover of rocks, shrubs, tree stumps, overhanging tree branches and unpalatable plants per plot. Data were analysed with Mann-Whitney U tests.

To estimate the impact of the cover of the five potential facilitative variables on sapling density, we fitted generalised linear models (GLM), with a negative binomial distribution and a log-ratio link function. Count data are generally analysed using Poisson distributions or, when variances exceed the means and when many cells are empty, negative binomial distributions (Krebs 1999). We ran these analyses for each site separately using all valid plots: 150 for site 1, 144 for site 2. When significant effects of an explanatory variable were found, Tukey's honestly significant differenced (HSD) tests were used to test for significance of differences between the different pairs of group means.

In order to get a final overview of the overall effects of the five potential facilitative elements on tree sapling density, we pooled data from the two sites together and run a GLM, again with a negative binomial distribution and a log-ratio link function. Here, we added "site" as an explanatory variable. Tukey's HSD tests were used for comparing pairs of group means of the significant variables.

We used Genstat 7 for the GLM's and SPSS release 11.5 for all other statistical analyses.

Results

Sapling recordings

We recorded a total of 433 established *Picea abies* saplings in the two sites. Most saplings measured 0 – 4 cm in height (70%), and were estimated to be 1 – 2 years old (personal observations). All other tree saplings (30%) were estimated to be over 2 years old. Saplings > 40 cm tall were few, but consistently present. This, together with observations of isolated small trees in the sites, suggests ongoing recruitment to larger size classes; some seedlings become saplings, and some saplings grow to maturity.

Differences between sites

Site 1 harboured more tree saplings than site 2 (Table 2). The range of sapling density per plot varied between 0 – 15 and 0 - 11 for site 1 and 2, respectively. Furthermore, sites differed in number of full plots (plots containing *Picea* saplings), sapling density per full plot and mean cover of rocks and shrubs (Mann-Whitney U tests, $p < 0.05$). Shrub cover was more common in site 1 than in site 2, while rock cover was generally higher in site 2. Tree stumps were relatively rare in both sites: only 11 plots contained stumps.

Table 2: Data on Picea abies saplings and facilitative structures at the two sites.

			Frequencies per cover type level						
Site	Cover type	Mean ± SD (%)	0%	0-1%	1-5%	5-25%	25-50%	50-75%	75-100%
1. La Sagne	Rock	3.88 ± 8.31	79	25	21	16	9	0	0
Plots ($4m^2$) = 150	Shrub	4.52 ± 15.21	119	11	4	5	4	5	2
No. of saplings = 343	Stump	0.73 ± 5.43	142	3	2	1	1	1	0
No. of full plots = 94	Tree branches	8.15 ± 18.0	96	7	11	16	11	6	3
Sapling density / full plot = 3.65 ± 3.05	Unpalatable	7.86 ± 9.65	25	28	40	43	14	0	0
2. Marchairuz	Rock	5.82 ± 11.44	31	45	37	21	6	4	0
Plots ($4m^2$) = 144	Shrub	0.91 ± 3.24	129	1	6	8	0	0	0
Nr. Saplings = 90	Stump	0.42 ± 3.12	141	2	1	0	0	0	0
Nr full plots = 45	Tree branches	9.16 ± 21.36	103	1	9	12	5	9	5
Sapling density / full plot = 2.00 ± 1.59	Unpalatable	7.36 ± 8.99	9	14	75	37	8	1	0

Effects of potential facilitative elements per site

The GLM's on sapling density per plot revealed significant positive effects of cover of rocks and unpalatables in site 1 and of cover of tree stumps in site 2 (Table 3). The significant models ($p < 0.001$, Chi-squared) explained 14.1% (site 1) and 12.4% (site 2) of the deviance. Reducing the models by leaving out variables stepwise did not improve the models (not shown). There were no significant interactions between the variables and they were therefore excluded from the models.

*Table 3: Results of generalised linear models, with a negative binomial distribution and a log-ratio link function, with tree sapling density per 4m2 plot as response variable, for each site (a, b) and with data pooled over sites (c). Independent predictor variables include percentage cover of rocks, unpalatables, shrubs, tree stumps, overhanging tree branches and site (2 vs 1). * p < 0.05, ** p < 0.01, *** p < 0.001.*

	Site 1 (n = 150)			Site 2 (n = 144)			Sites 1+2 (n = 294)		
Parameter	Estimate + SE	*df*	*t*	Estimate + SE	*df*	*t*	Estimate + SE	*df*	*t*
Constant	–0.515 ± 0.055	1	–9.32 ***	–1.167 ± 0.131	1	–8.94 ***	–0.546 ± 0.054	1	–10.11 ***
Site							–0.575 ± 0.084	1	–6.81 ***
Rocks	0.009 ± 0.002	1	4.87 ***	0.008 ± 0.005	1	1.55	0.010 ± 0.002	1	5.80 ***
Unpalatables	0.008 ± 0.002	1	3.18 ***	0.008 ± 0.008	1	1.10	0.009 ± 0.002	1	3.74 ***
Shrubs	–0.002 ± 0.003	1	–0.79	0.018 ± 0.018	1	1.01	–0.003 ± 0.002	1	–1.07
Stumps	0.004 ± 0.004	1	1.16	0.027 ± 0.005	1	4.93 ***	0.271 ± 0.097	1	2.79 **
Branches	0.0005 ± 0.002	1	0.27	–0.003 ± 0.005	1	–0.58	0.001 ± 0.002	1	0.17

When comparing the means of between levels for each significant factor using Tukey's HSD test, we found a higher sapling density at the higher cover levels of rock, unpalatable, and tree stump cover. At site 1, plots with a rock cover of ≥ 10%, and an unpalatable cover of ≥ 25% contained more *Picea* saplings. At site 2, plots with tree stump cover had a higher mean sapling density than plots without.

Effects of potential facilitative elements, pooled over sites

Analysis of the pooled data (over both sites) revealed significant effects of site and rock-, unpalatable- and tree stump cover on sapling density (Table 3). The significant model ($p < 0.001$, Chi-squared) explained 24.84% of the deviance. Sapling density was significantly higher in site 1. Figure 1 shows the effects per level of cover on saplings density: plots with a higher cover of rocks, unpalatables and tree stumps contained a higher sapling density.

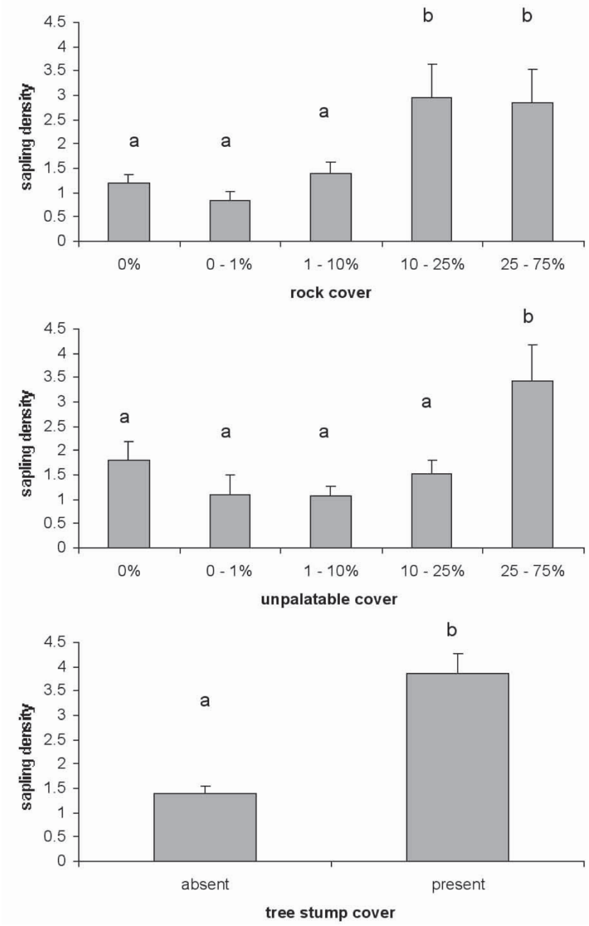

Figure 1: Mean sapling density (+se) per plot for each level of the significant factors unpalatable- and rock cover. Data are pooled over both sites. Different letters indicate statistically significant differences at p < 0.05 (Tukey HSD test).

Discussion

Spatial associations and selective grazing

In this study we found that plots with higher cover of rocky outcrops, unpalatable plants and tree stumps were more likely to contain *Picea* saplings than plots with no or low cover of these. This was true despite differences between the sites in grazing system (free ranging *versus* rotation), grazing intensity, altitude and climatic factors (Table 1). Although we are well aware of the constraints of the correlative nature of this study, these results suggest that spatial associations of *Picea* recruitment with unpalatable plants, rocky outcrops and tree stumps may be a general feature in wooded pasture ecosystems. This pattern could reflect positive effects on tree saplings by unpalatable plants, rocky outcrops and tree stumps as an indirect effect of selective grazing behaviour. Foraging behaviour studies have shown that ungulates generally graze selectively and concentrate on short, leafy swards containing relatively high nutrient concentrations (Wallis deVries et al. 1999). Patches of little nutritious value, and so avoided, often occur on rocky shallow soils, tree stumps or where unpalatable plants are prevalent. Tree saplings establishing in or near such patches could, therefore, be protected against both trampling and grazing by large herbivores, as has also been proposed by other authors in studies on grazed ecosystems (Vera 2004, Rousset & Lepart 2000). Most of these studies, however, focussed on spatial associations of palatable tree species (*Quercus* spec.) with shrubs in grazed environments, and experimental evidence concerning mechanisms for this association is still scarce (but see Bakker et al 2004). Here, we show an example of spatial associations of a tree species (*Picea abies*) in its sapling phase with unpalatable, high-statured herbaceous or woody plants, rocky outcrops and tree stumps in a grazed system. It seems that even relatively unpalatable tree species like *Picea* may benefit from associational resistance: cattle may browse unprotected saplings by chance because of their tasty surroundings and avoid an unpalatable patch with a luckier sapling.

We also expected to find a higher sapling density in plots with a higher cover of potential facilitative structures, assuming that these would offer a) a larger suitable area for tree seeds to arrive, germinate and establish and b) a better protection against the cattle. A higher sapling density in plots with a high cover of nurse structures could furthermore indicate that the proportional cover of nurse structures per plot has an influence on the selection behaviour of cattle. Our data show evidence for these expectations, as plots with tree stumps and a higher cover of rocky outcrops and unpalatable plants had higher sapling densities.

According to two succession models (Bokdam et al. 2001, Olff et al. 1999) woody invasion in grazed grasslands will start after reduced grazing pressure, induced by declining palatability of the lawn species (i.e. mostly grasses and sedges). We did not consider the effects of these smaller species in this study. Nevertheless, preliminary results of another experiment in the same study sites showed that some of these smaller unpalatable species are significantly more often present near *Picea abies* saplings than in plots without these (unpubl.). This would indicate that associational resistance may also be active at a smaller scale, involving subordinate herbs.

Other potential processes involved

Besides selective herbivory there are, however, a few alternative explanations for the observed spatial distribution of *Picea* saplings. Some studies on spatial distribution of seeds and saplings report both nursing- and seed trapping effects (de Viana et al. 2001, Weltzin & McPherson 1999). Both an increased seed input near tall (nurse) structures via the catching in of seeds (seed trapping) and improved germination conditions under the canopy of nurse structures led to a relatively higher density of seeds and saplings. Others (Jurena & Archer 2003) report that above- and below ground gaps in the grass layer were the main contributors to tree sapling establishment. In our studied system, rocky outcrops, unpalatable plants and tree stumps may act as seed traps for the mainly wind dispersed *Picea abies* seeds, or form particularly suitable microsites for seed germination.

Although tree stumps only occurred in 11 out of the 294 plots, they appeared to have particularly strong positive effects on sapling density. All these plots contained tree saplings, with a density of 2 – 6 saplings per plot. Similar positive effects of tree stumps, roots and logs on *Picea* regeneration were found in boreal swamp forests in Sweden, where the elevated micro relief with rotten wood offered saplings favourable moisture, aeration, light conditions, nutrients, mycorrhizal fungi and absence of resource competition with other plants (Hörnberg et al 1997). However, these boreal forests were not grazed, and the protective role of tree stumps against herbivory may be an additional factor.

Rock outcrops could, besides offering physical protection, improve the conditions for *Picea* seeds and seedlings by affecting local temperature. In early spring, rocky outcrops generally warm up faster than their environment, causing local snowmelt, which may favour germination of seeds. In addition, established seedlings may profit from a prolonged growing season near rocky outcrops in this relatively harsh environment.

The observed associations of established *Picea* saplings with unpalatable plants, rocky outcrops and tree stumps could, hence, be caused by several processes. However, since we excluded newly emerged seedlings (< 1 year old) from recording and found tree saplings of variable height classes in close proximity to the three types of structures, it is unlikely that we observed only the effects of germination improvement. Clearly, more research is needed to further investigate and disentangle the mechanisms contributing to the observed spatial associations of the *Picea abies* saplings. Nevertheless, we conclude that unpalatable plant species, rocky outcrops and tree stumps can have positive effects for *Picea abies* recruitment in wooded pastures of the Swiss Jura Mountains. The observed spatial associations are consistent with the shifting mosaic cycle from open grasslands to woodlands. Experiments to further test the associational resistance hypothesis are presently underway.

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CHAPTER 2

Facilitation of tree recruitment in wood-pastures: beyond species-species interactions

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Abstract

Question: Can local plant communities as a whole, rather than individual unpalatable species, enhance tree recruitment in wood-pastures after accounting for local environmental conditions? To what extent is facilitation a species-specific interaction?

Location: Two wood-pastures located in the Swiss Jura Mountains

Methods: Vegetation data (species occurrence, abundance and height) was collected at two one-hectare study sites in 1m2 plots with either small (< 5 cm), big (< 40 cm) or no Picea abies saplings. In addition, the cover of unpalatable species and environmental descriptors (microtopography, soil depth, soil pH, light) were recorded. In a generalized linear model (GLM) predicting the number of tree saplings, we sequentially added these environmental variables, unpalatable plant cover and, finally, a community variable derived after NMDS summarizing the main compositional gradient of the vegetation.

Results: Species associated with saplings, as well as the direction of the associations, differed between sites. Convex microtopography, elevated pH and shallow soil were positively related to sapling occurrence. The cover of unpalatable species did not further explain the residuals of the model. However, the plant community variable improved the accuracy of the model for both sites.

Conclusions: Both the abiotic environment and neighbouring species were related to the presence of Picea saplings. We suggest that local plant communities may influence tree recruitment in grazed ecosystems beyond simple pairwise species interactions, independent of direct abiotic factors.

Keywords: *Picea abies*, fidelity, plant species associations, compositional data analysis, NMDS, GLM.

Nomenclature: Tutin et al. (1964-1980)

Introduction

In the face of global change and biological invasions, active intervention is more often required for species conservation and landscape maintenance (Hooper et al. 2005), but management is hampered by our inability to predict the invasion or persistence of key species. Reversing undesirable changes in community compositions is one of the major challenges of restoration ecology. Due to their large size, trees modify the abiotic environment, create habitat for numerous species and interact with many neighbours. In this sense, trees can be considered as foundation species (*sensu* Bruno et al. 2003). Their establishment is therefore a key process in the landscape and understanding the mechanisms involved is crucial for species maintenance and sustainable management.

Among coexisting plant species, the inevitable competition for space, light and soil resources will affect the establishment of individuals (Bengtsson et al. 1994). An individual's competitive ability varies with life stage, and conventional studies of relative competitive ability shed little light on the factors affecting plant establishment in natural and semi-natural environments. In particular, young plants are generally poor competitors for space against larger, established individuals, irrespective of species. In such cases, young plants establish only in favourable microsites. Facilitator species reduce environmental or competitive stress; in many communities, facilitation affects plant establishment and therefore has strong influences on species coexistence and spatial patterns (Bertness & Callaway 1994, Callaway 1995, Tirado & Pugnaire 2005). Such positive interactions among species include amelioration of environmental conditions (Oesterheld & Oyarzabal 2004), protection from grazing due to unpalatability (Callaway et al. 2005), resource improvement (Walker et al. 2003), and reduced competition (Hacker & Gaines 1997). Facilitation has been shown to be important for establishment of key species, including trees regenerating in an herbaceous layer (Davis et al. 1998, Pagès & Michalet 2003, Smit et al. 2006), and invasive species colonizing new communities (Woitke & Dietz 2002, Vila & Weiner 2004). Such positive interactions among neighbouring plants are only detectable when their strength exceeds the strength of negative interactions, because in general only net effects are measurable (Brooker & Callaghan 1998, Bruno et al. 2003). These net effects ultimately determine species assemblages and community structures of ecosystems.

Experimental studies on facilitation usually focus on pairwise species interactions in simplified ecological systems. Neighbouring species, environmental conditions, and site history are controlled to be as similar as possible. This maximizes the power of the test but, outside a realistic ecological context, it is difficult to generalize the results into insights on the process in natural systems (Bruno et al. 2003). Species are obviously not all of the same importance in structuring plant communities (Magurran 2005), and while species-species interactions clearly play an important role, in some cases the species to which facilitator organisms belong may not be relevant. For example, in a system where nurse plants protect seedlings from grazing, the effects of different species of nurse plants may be the same as long as they are all avoided by grazers. Based on studies on species interactions in a semi-arid shrubland, Riginos et al. (2005) suggested that the characteristics of species, including life-history strategies, are likely to have important effects on the outcome of their interactions. This raises the possibility of functional equivalence among species (Hubbell 2005) in producing facilitative effects.

We suggest that the importance of site context (including community composition and structure, environmental conditions and site history) in facilitation has been underestimated, due to the intractability of the problem in an experimental perspective. To investigate this possible context-dependency of facilitation, we focus on tree sapling establishment in *Picea abies*-dominated wood-pastures of the Swiss Jura Mountains. Positive associations with nurse structures and plants have been shown to facilitate tree sapling establishment and survival in this system (Smit et al. 2005). A correlative study was carried out in two pastures, focussing on *Picea abies* saplings of more than one year old, growing within the herbaceous layer. Positive associations between tree saplings and plant species were considered as indicative for facilitation. We explore the following hypotheses: (i) at a given site and at an observation scale of 1 m^2, tree recruitment is dependent on the local plant community, even after accounting for the effect of local environmental conditions and individual unpalatable species with facilitative effects; (ii) the balance between positive and negative interactions may change for a given species depending on overall site conditions and history; (iii) different species could play the same facilitative role depending on the site.

Material and Methods

Study sites

The study was carried out in two contrasting wood-pastures of the Swiss Jura Mountains where facilitation processes on tree regeneration were previously studied (Smit et al. 2005). At the Marchairuz site (Pré-aux-Veaux, Le Vaud VD, altitude 1340 m a.s.l., 6°12’E, 46°32’N), *Picea abies* is the only dominant tree species. The geomorphological heterogeneity is high, with abundant calcareous outcrops generating microtopography of hummocks and hollows. In local depressions, allochthonous loess depositions from the last ice period result in more acidic conditions (pH 4.3) compared to the alkaline conditions of surrounding shallow soils (pH 7.7), allowing acidophilous species to establish despite the calcareous rock base (Havlicek & Gobat 1996). At the La Sagne site (Communal, La Sagne NE, altitude 1150 m a.s.l., 6°48’E, 47°02’N), *Picea abies* grows in association with *Fagus sylvatica* and *Acer pseudoplatanus*. The geomorphology is similar to the first site, but with coarser grain. Both sites have been continuously used for summer grazing by cattle for at least a century. See Smit et al. (2005) for a detailed site description.

In each site, we selected a study area of one hectare with an overall tree cover of 30% in Marchairuz and 40% in La Sagne.

Data collection

Field work was carried out between July and October 2002. From a preliminary inventory of 600 1-m^2 plots regularly distributed over the entire one-ha study area, 71 (Marchairuz) and 70 (La Sagne) plots were selected using a stratified random sampling design covering the following situations: (i) at least one “big” *Picea* sapling, with heights ranging between 5 and 40 cm; (ii) at least one “small” *Picea* sapling, with heights not exceeding 5 cm (> 1 year old); (iii) “empty” plots with no *Picea* sapling (Table 1).

In each plot, a vegetation survey was performed for herbaceous plants and shrubs, including a species list and the visual estimation of the percentage cover for each species using the dominance codes of Braun-Blanquet (1964). Relative species cover was then calculated from dominance codes by adjusting the sum for each sample to 100% in order to represent the contribution of each species to the surrounding plant community. Additionally, a height dominance index was recorded for each species, which is a visual estimation of the average height of the foliage to the nearest 5 cm above the ground surface. The relative cover value was then multiplied by the height dominance index, giving a volumic dominance value for each species, interpreted as an estimate of the relative biovolume occupied by each species within the plant community.

Due to their functional importance in grazed systems, unpalatable species were grouped into one single variable (unpalatable) by summing their biovolume in each sample. The list of unpalatable species was derived from the literature and personal observations, and included all species with clear mechanical defences like spines and thorns or with well-documented toxic chemical compounds. These were *Carlina acaulis*, *Cirsium acaule*, *Cirsium arvense*, *Crataegus monogyna*, *Rosa* sp. pl., *Rubus* sp. pl., *Juniperus communis* (mechanical defences), *Atropa belladonna*, *Epilobium montanum*, *Gentiana lutea*, *Helleborus foetidus*, *Orchis mascula*, *Ranunculus* sp. pl. (chemical defences).

In each plot, the following environmental descriptors were collected: (i) the microtopography described on a three-level scale (-1 = concave; 0 = flat; 1 = convex); (ii) the slope derived from horizontal distance and vertical elevation measures; (iii) the mean depth from the ground level to the calcareous rock substrate (hereafter mean soil depth) calculated as the average of the measures made at each corner, at the middle point of each side and at the centre point of the plot, using a metal stick; (iv) the mean soil water pH, derived from two samples per plot using standard methods (Anderson & Ingram 1993) ; (v) the total potential hours of sunlight over the growing season (May to October) measured using a solar compass (Herzog Forsttechnik AG, Switzerland), in order to estimate the shading effect of the neighbouring trees.

Data analysis

To analyse the structure of the vegetation dataset and to extract a community descriptor, a non-metric multidimensional scaling (NMDS) (Cox & Cox 2001) was applied to the Euclidean distance matrix between samples (Legendre & Legendre 1998), using the log-transformed biovolume values. This method was selected because it has been found to be the best ordination method for detecting vegetation gradients (Minchin 1987) and therefore most adequate for using the coordinates on the first ordination axis as a one-dimensional community descriptor.

NMDS is a mapping technique which aims at representing the data in few dimensions (here two axes), so that distances in the reduced space reflect the distances between sample plots as closely as possible (Cox & Cox 2001). It is an iterative procedure starting from an initial configuration (at first from the results of a principal coordinate analysis) and further results are retained when better than previous solutions, by minimizing an objective stress criterion. To prevent convergence toward a local solution, the analysis was repeated with ten random starting configurations. Hence, the two-dimensional configuration could be presented graphically in the same way as in correspondence analysis (terBraak 1986), except that only configuration is meaningful whereas direction, scale and origin of each axis are arbitrary.

Generally used between the configurations of two ordinations (Peres-Neto & Jackson 2001), the Procrustes rotation method (Gower 1971) was applied here between the NMDS scores and the number of saplings in each corresponding plot. It uses uniform scaling and rotation to minimize the squared differences between these two data sets, displaying on the first axis of the transformed NMDS the best discrimination of the plots according to the number of saplings they host. NMDS plot scores on the first ordination axis after Procrustes rotation were taken as the one-dimensional descriptor of the local plant community for further analyses. The multidimensional space of the community matrix was thus reduced to a single variable Veg1 representing the compositional gradient linked to sapling abundance. After fitting a Generalized Additive Model (GAM) (Green & Silverman 1994), a smooth surface using thinplate splines on the number of saplings was displayed on the ordination plot, as well as the plant species scores.

Count data are generally analysed using Poisson distributions or, when variances exceed the means and when plot scores contain many zeros, negative binomial distributions (Krebs 1999). To assess the effects of abiotic environmental variables on the number of *Picea* saplings in each site we first fitted generalised linear models (GLM) with a negative binomial distribution and a log-ratio link function. The significance of the model components was tested using an analysis of variance (ANOVA). In a second step, we estimated the remaining impact of the unpalatable species and of the compositional gradient on the response variable (number of saplings), after accounting for the effect of the local abiotic environment. As GLM includes sequentially the given variables, we first fitted the abiotic environmental variables (Table 1). Then we fitted the unpalatable variable to the residuals of this environmental model in order to assess remaining effects of the unpalatable species within the plots. The Veg1 variable was finally added to the model, to test for remaining effects of the whole plant community (Table 1).

All analyses were performed separately for each site with R 2.4.0 (R Development Core Team 2006). NMDS were performed using the isoMDS function in MASS library, the Procrustes rotation with the procrustes function in vegan library.

Results

We recorded a total of 76 saplings in Marchairuz and 162 in La Sagne, in 71 and 70 1m^2-plots, respectively. Saplings were between 1.5 and 40 cm high. In Marchairuz, microtopography was more heterogeneous: hummock and hollow conditions were frequent, together with globally shallower soils (Table 1). Plant species richness was higher in Marchairuz, with a mean of 40.7 species per square meter in plots with *Picea* regeneration (33.8 species

Table 1: Picea regeneration success, abiotic environmental conditions and vegetation structure observed in the 1-m² plots of the two study sites (number of plots for qualitative variables, mean ± 1 SD for quantitative variables).

	Variable (unit)		Marchairuz			La Sagne		
	Plot type		empty	small	big	empty	small	big
			n=29	*n=21*	*n=21*	*n=30*	*n=23*	*n=17*
Spruce saplings	Number of saplings	0:	n=29	-	-	n=30	-	-
		1:	-	n=6	n=2	-	n=6	n=1
		≥2:	-	n=15	n=19	-	n=17	n=16
	Maximal height (cm)		-	3.86 ± 0.91	8.07 ± 3.03	-	3.41 ± 1.13	9.47 ± 6.16
Environmental descriptors	Microtopography	concave (-1):	n=10	n=4	n=0	n=1	n=2	n=0
		flat (0):	n=16	n=8	n=2	n=26	n=15	n=13
		convex (1):	n=3	n=9	n=19	n=3	n=5	n=4
	Slope (%)		12.8 ± 9.5	19.3 ± 11.4	16.7 ± 9.7	17.0 ± 11.0	18.7 ± 8.9	16.5 ± 7.7
	Average soil depth (cm)		14.3 ± 8.0	10.5 ± 4.5	8.3 ± 4.4	27.0 ± 12.5	18.9 ± 9.4	18.5 ± 5.7
	Soil pH (H_2O)		5.91 ± 0.78	6.55 ± 0.59	6.64 ± 0.33	-	-	-
Vegetation	Shrub cover (%)		1.2 ± 5.6	0	0	16.3 ± 33.2	8.0 ± 25.3	13.2 ± 27.2
	Total moss cover (%)		14.1 ± 18.9	11.8 ± 13.4	11.0 ± 11.3	22.6 ± 27.1	17.8 ± 16.3	27.8 ± 31.2
	Plant species richness per plot		33.8 ± 8.8	40.7 ± 8.4	40.6 ± 6.0	28.0 ± 5.6	30.4 ± 5.0	26.3 ± 6.7
	Total vascular plant cover (%)		87.1 ± 16.4	86.5 ± 16.7	89.8 ± 9.7	79.3 ± 28.5	84.0 ± 22.9	63.5 ± 29.2

for “empty” plots), compared to La Sagne where plots with *Picea* saplings hosted a mean of 28.7 species (28.0 species for “empty” plots; Table 1).

On the NMDS ordination, the vegetation gradient clearly sorted species associated with *Picea* saplings from negative to positive. These species were however quite different between sites: in the Marchairuz site, *Nardus stricta*, *Luzula multiflora*, *Trifolium repens*, *Achillea millefolium*, *Veronica chamaedrys* and *V. officinalis* were negatively associated with *Picea* saplings, whereas *Gentiana lutea*, *Aquilegia atrata*, *Acinos alpinus*, *Gymnadenia conopsea* and *Daphne cneorum* were positively associated with *Picea* saplings (Figure 1). On the other hand, in La Sagne, *Gentiana lutea*, *Bellis perennis*, *Stellaria graminea*, *Briza media* and *Lotus corniculatus* were negatively associated with *Picea* saplings, whereas *Carex flacca*, *Fragaria vesca*, *Galium rotundifolium*, *Hieracium murorum* and *Viola reichenbachiana* were positively associated with *Picea* saplings (Figure 2).

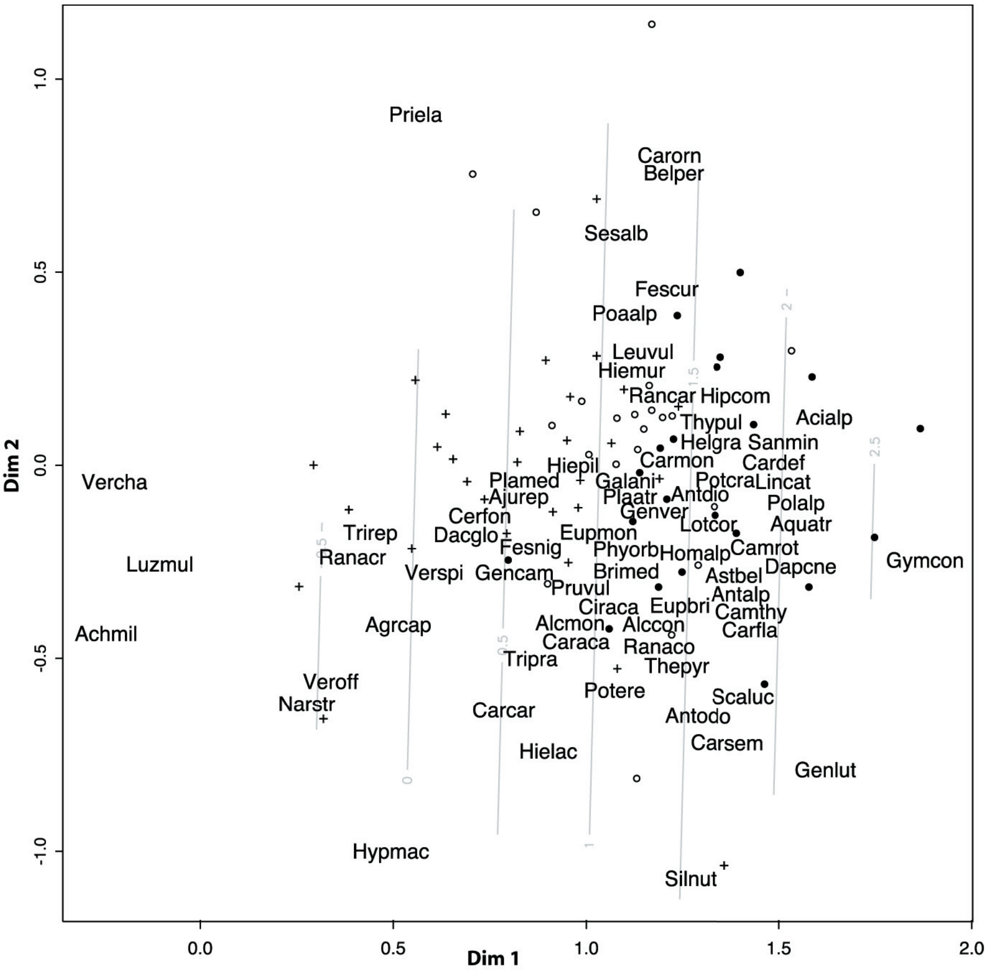

Figure 1: Bidimensional NMDS ordination plot of the samples and the species at Marchairuz site, after Procrustes rotation. Converging stress value = 22.495. A smooth surface using thinplate spline interpolating the number of saplings is added. Only species with frequency > 10% are displayed (+ = plot type "empty"; empty circle: plot type "small"; full circle: plot type "big"). See appendix 1 for the list of species abbreviations.

The stepwise selection of the environmental variables retained microtopography, soil pH and shrub cover for the Marchairuz site and microtopography, soil depth and slope for the La Sagne site. Adding these variables sequentially in the GLM showed a clear effect of microtopography on the number of *Picea* saplings in both sites (Table 2). Furthermore, the residuals of the microtopography model can partly be explained by the soil pH in the case of Marchairuz, and by the soil depth in the case of La Sagne (Table 2). Concretely, elevated microtopographical positions were favourable for *Picea* saplings, as well as high soil pH or shallow soil, depending on the site.

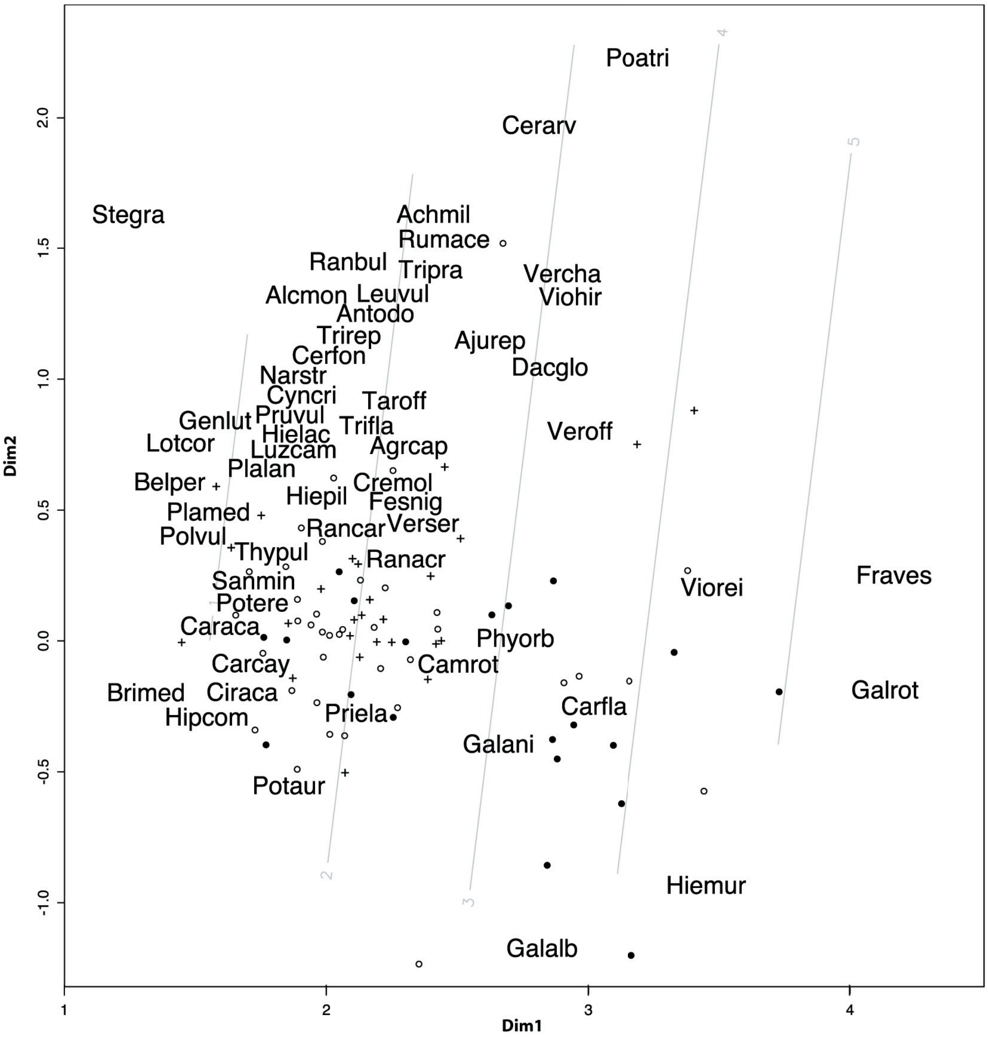

Figure 2: Bidimensional NMDS ordination plot of the species at La Sagne site, after Procrustes rotation. Converging stress value = 18.837. A smooth surface using thinplate spline interpolating the number of saplings is added. Only species with frequency > 10% are displayed (+ = plot type "empty"; empty circle: plot type "small"; full circle: plot type "big"). See appendix 1 for the list of species abbreviations.

Finally, the biovolume of unpalatable plant species did not further explain the residuals of the model containing the three corresponding abiotic environmental variables for each site. However, the vegetation community descriptor Veg1 clearly contributed to the improvement of the regeneration conditions of *Picea* in both sites (Table 2). Including this one-dimensional vegetation community descriptor in the final model significantly improved the accuracy of the prediction.

*Table 2: ANOVA tests on the components of generalised linear models (GLM) with a negative binomial distribution and a log-ratio link function of local abiotic environment, unpalatable and local plant community descriptor Veg1 determining the number of Picea saplings. (n.s. = not significant; * = P < 0.05; ** = P < 0.01; *** = P < 0.001).*

Parameter	*df*	deviance resid.	resid. *df*	resid. deviance	p-value
			site 1 - Marchairuz		
NULL			70	103.86	
Microtopography	1	21.86	69	82.00	2.93e-06 ***
Mean soil depth	1	3.09	68	78.91	0.079 n.s.
pH (water)	1	3.93	67	74.97	0.047 *
Slope	1	0.17	66	74.80	0.679 n.s.
Sun light duration	1	0.30	65	74.50	0.585 n.s.
Unpalatable (cover)	1	0.59	64	73.91	0.441 n.s.
Veg1	1	9.83	63	64.08	0.002 **
			site 2 - La Sagne		
NULL			69	106.46	
Microtopography	1	6.38	68	100.09	0.012 *
Mean soil depth	1	17.46	67	82.62	2.93e-05 ***
Slope	1	1.36	66	81.27	0.244 n.s.
Sun light duration	1	0.21	65	81.06	0.647 n.s.
Unpalatable (cover)	1	0.18	64	80.88	0.673 n.s.
Veg1	1	6.25	63	74.62	0.012 *

Discussion

Our study clearly indicates effects of the abiotic environment on the occurrence of *Picea* saplings which supports the environmental determinism of tree regeneration as shown by others (e.g., Kuuluvainen 1994, Pagès & Michalet 2003, Veblen 1989). In both contrasting study sites, elevated microtopography was favourable to the establishment of *Picea*. Comparable studies in boreal forests showed similar results for conifer trees (Kuuluvainen 1994, StHilaire & Leopold 1995). In our study sites, elevated positions are mainly due to a fine-grain geological heterogeneity, and often correspond to shallow soils and, sometimes, to rock outcrops. The sensitivity to drought is higher in these exposed microsites, and snow cover, lasting four to five months in winter, disappears earlier on such elevated positions in spring which influences microclimate and plant growth. Hence, such suggests both direct and indirect effects of microtopography on the occurrence of *Picea* saplings, directly by altered light and moisture and indirectly through interactions with the herbaceous vegetation influenced by such conditions (Holtmeier & Broll 1992, Milchunas & Noy-Meir 2002).

The herbaceous plant community at fine scale appears to play an important role for the occurrence of *Picea* saplings given the large variation explained by the local abiotic environment (Table 2). This result supports previous hypotheses on the role of facilitation and competition within the herbaceous layer on tree regeneration in wood-pastures (Smit et al. 2005), and justifies the increasing recognition of the importance of these biotic interactions in plant communities. But our study also reveals that, in contrast with usual conclusions on grazed ecosystems, this community effect is not just due to some unpalatable species which here explain only very little of the sapling occurrence after accounting for abiotic filtering. In fact, in accordance with our hypothesis, we show that many other species should be involved in the direct and indirect interactions that enable tree recruitment.

The influence of the herb community surrounding the tree sapling in a 1-m^2 plot was summarized into a one-dimensional gradient descriptor Veg1. In the Marchairuz site, the unpalatable species *Gentiana lutea*, *Aquilegia atrata*, *Gymnadenia conopsea*, and *Daphne cneorum* show a strong positive association with tree regeneration (Figure 1). This reveals the role of these few species as refuges in a grazed environment, and confirms the role of associational resistance in the early stages of the regeneration of *Picea*. Furthermore, strong competitors or fast growing plant species (*Nardus stricta*, *Trifolium repens*, *Veronica officinalis*, *V. chamaedrys*, *Bellis perennis*) show strong negative associations with *Picea* saplings. This can be interpreted as competitive exclusion by these dominant species.

A comparison of species among sites sheds a light on the species specificity of the associations. *Gentiana lutea*, an a priori unpalatable species, showed a positive association with tree regeneration in one site (Marchairuz) and a negative association in another (La Sagne). This is in accordance with our second hypothesis. It reveals the specificity of associational resistance and shows the possible determinant role of site conditions and surrounding plant communities in the expression of positive (or negative) associations. Such net expression of potentially positive associations has already been shown by Riginos et al. (2005) between shrub seedlings and adults to depend on abiotic conditions. Furthermore in grazed systems, the studies of Rebollo et al. (2005) and Smit et al. (in press) show how grazing intensity determines the net outcome of species-species interactions expected to be facilitative. Hence, the role of facilitation driving plant communities in natural ecosystems may be nuanced by the role external factors play in its net expression.

Our results indicate that the majority of the species play an intermediate role, being either facilitators or competitors, depending on the competitive ability within the community and on the general site conditions. Even potentially toxic plants in pastures, which would a priori be browsing refuges, could generate competitive exclusion of tree saplings. Some species that are strong competitors (i.e. *Nardus stricta* and *Trifolium repens*) were negatively associated with *Picea* saplings, whereas the slow-growing *Fragaria vesca*, *Hieracium murorum*, *Carex flacca* and *Acinos alpinus* showed strong positive associations.

This variable position of some species on the community gradient related with tree regeneration suggests that their influence on the overall effects predominantly attributed to species-specific interactions has possibly been overestimated in previous studies. Our results support the hypothesis that the community surrounding an establishing immigrant species has a net effect that is not necessarily dominated by a few species with a highly specific function, such as unpalatability, of which even the effect is highly dependent on the context (Milchunas & Noy-Meir 2002). Therefore, we suggest a less species-specific influence of plant communities on establishing tree saplings. As a possible consequence, species could be exchangeable in their functional position towards tree regeneration. In this sense, this would support our third hypothesis of a possible functional equivalence of species in community dynamics (Hubbell 2005; Zamora 2000).

The natural constraints on immigrating species or regenerating trees are numerous and of very different kinds. They act in both direct and indirect ways on the probability of establishment and survival of small saplings, which reveals the complexity of natural systems. Biotic interactions with plants, herbivores and soil microorganisms interplay together with the abiotic environment within the wood-pasture ecosystem and so contribute to a suitable regeneration niche for *Picea* saplings. In such a context, experimental studies focussing on specific processes and simplified systems may show intrinsic limits, and observational studies in real complex systems remain very effective.

Concluding, plant communities taken as a whole might have specific functional roles for determining establishment niches for plant species. In a natural multi-species context, the assemblage of species will contribute to the persistence of establishing or invasive species, and our results suggest that the functional role of species assemblages is not necessarily dominated by a few functionally well identified species. Species might become less important compared to synusiae and phytocoenoses, which might even be considered as the most adequate functional units in vegetation dynamics, as was proven for wood-pastures (Gillet & Gallandat 1996, Gillet et al. 2002).

Could the community effects on tree establishment be an emergent property, partly independently from few functionally well-defined individual species of the community itself? Our results support at least the opportunity to consider plant communities as possible pertinent focus level for understanding functional dynamics driving tree regeneration.

Acknowledgements

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Appendix 1 – abbreviation list of plant species used in the figures.

Achmil = *Achillea millefolium*; Acialp = *Acinos alpinus*; Agrcap = *Agrostis capillaris*; Aju rep = *Ajuga reptans*; Alccon = *Alchemilla conjuncta*; Alcmon = *Alchemilla monticola*; Antalp = *Anthyllis vulneraria* subsp. *alpestris*; Antdio = *Antennaria dioica*; Antodo = *Anthoxanthum odoratum*; Aquatr = *Aquilegia atrata*; Astbel = *Aster bellidiastrum*; Belper = *Bellis perennis*; Brimed = *Briza media*; Camrot = *Campanula rotundifolia*; Camthy = *Campanula thyrsoides*; Caraca = *Carlina acaulis*; Carcar = *Carum carvi*; Carcay = *Carex caryophyllea*; Cardef = *Carduus defloratus*; Carfla = *Carex flacca*; Carmon = *Carex montana*; Carorn = *Carex ornithopoda*; Carsem = *Carex sempervirens*; Cerarv = *Cerastium arvense*; Cerfon = *Cerastium fontanum* subsp. *triviale*;

Ciraca = *Cirsium acaule*; Cremol = *Crepis mollis*; Cyncri = *Cynosurus cristatus*; Dacglo = *Dactylis glomerata*; Dapcne = *Daphne cneorum*; Erialp = *Erigeron alpinus*; Eupbri = *Euphorbia brittingeri*; Eupmon = *Euphrasia rostkoviana* subsp. *montana*; Fesnig = *Festuca nigrescens*; Fescur = *Festuca curvula*; Fraves = *Fragaria vesca*; Galalb = *Galium album*; Galani = *Galium anisophyllon*; Galrot = *Galium rotundifolium*; Gencam = *Gentianella campestris*; Genlut = *Gentiana lutea*; Genver = *Gentiana verna*; Gymcon = *Gymnadenia conopsea*; Helnum = *Helianthemum nummularium* subsp. *grandiflorum*; Hielac = *Hieracium lactucella*; Hiemur = *Hieracium murorum*; Hiepil = *Hieracium pilosella*; Hipcom = *Hippocrepis comosa*; Homalp = *Homogyne alpina*; Hypmac = *Hypericum maculatum*; Leuvul = *Leucanthemum vulgare*; Lincat = *Linum catharticum*; Lotcor = *Lotus corniculatus*; Luzcam = *Luzula campestris*; Luzmul = *Luzula multiflora*; Narstr = *Nardus stricta*; Phyorb = *Phyteuma orbiculare*; Plaatr = *Plantago atrata*; Plalan = *Plantago lanceolata*; Plamed = *Plantago media*; Poaalp = *Poa alpina*; Poatri = *Poa trivialis*; Polalp = *Polygala alpestris*; Polvul = *Polygala vulgaris*; Potaur = *Potentilla aurea*; Potcra = *Potentilla crantzii*; Potere = *Potentilla erecta*; Priela = *Primula elatior*; Priver = *Primula veris*; Pruvul = *Prunella vulgaris*; Ranaco = *Ranunculus aconitifolius*; Ranacr = *Ranunculus acris* subsp. *friesianus*; Ranbul = *Ranunculus bulbosus*; Rancar = *Ranunculus carinthiacus*; Rumace = *Rumex acetosa*; Sanmin = *Sanguisorba minor*; Scaluc = *Scabiosa lucida*; Sesalb = *Sesleria albicans*; Silnut = *Silene nutans*; Stegra = *Stellaria graminea*; Taroff = *Taraxacum officinale*; Thepyr = *Thesium pyrenaicum*; Thypul = *Thymus pulegioides*; Trifla = *Trisetum flavesens*; Tripra = *Trifolium pratense*; Trirep = *Trifolium repens*; Vacmyr = *Vaccinium myrtillus*; Valmon = *Valeriana montana*; Vercha = *Veronica chamaedrys*; Veroff = *Veronica officinalis*; Verser = *Veronica serpyllifolia*; Verspi = *Veronica spicata*; Viohir = *Viola hirta*; Viorei = *Viola reichenbachiana*.

CHAPTER 3

The identity of facilitator species vanishes at small scale: the case of tree regeneration in grasslands

Introduction

The understanding of biological interactions is fundamental in ecological research, do they concern parts of organisms, individual species, biological communities or entire ecosystems (Loreau et al. 2001). From the results of previous studies, ecologists generally build a conceptual model of the system and the processes, including a definition of the major functional units which will underlay further assessments. This leads them to expect a particular behaviour of the system or specific results out of the experiments or observations. The point of view and the theoretical background of the observer play therefore a critical role on the interpretation of the results, generating the most passionate debates and setting the basis of personal expertise.

It is now well recognized that biological processes operate at given scales, defined by their intrinsic grain and extent, and consequently by the optimal resolution at which resulting effects can be stated and observed (Dale 1999, Turner et al. 2001). Describing processes or resulting patterns supposes therefore to adjust the resolution at which the observations are made to the scale at which the focus process is supposed to work dominantly (Carlile et al. 1989). Literature and research interest on scale aspects raised over the last few decades (Petraitis and Latham 1999, Klimes et al. 2001, Dungan et al. 2002, Van de Koppel et al. 2005). The question of scale became a predominant concern in understanding ecological processes, and often challenges ecologists in interpreting their results (e.g., Amarasekare 2000, Loreau et al. 2001, de Blois et al. 2002).

Despite these recent preoccupations, an explicit definition of the relevant scale in relation to processes is often missing in current research including experimental studies known to be closer to processes. The major attempts belong to ecological modelling (Feagin et al. 2005) or landscape ecology (de Blois et al. 2002), where the question of scale has to be faced more directly. Observational and experimental studies testing the scale effect as the first step of research are scarce and standard resolution sizes are often taken first to be comparable with other studies. This tendency seems even to increase when observed results are used mainly to confirm existing findings. Knowing that an inappropriate scale for observation or analysis may lead to a misinterpretation of the results (Dungan et al. 2002), this scale issue related to patterns and processes is of major importance.

Spatial dynamics of plant communities have been investigated at various spatial resolutions, ranging from centimetres to kilometres (van der Maarel & Sykes 1993, Purves & Law 2002, Okland & Bakkestuen 2004). The processes to be investigated depend on the scale, ranging from local response under stress or competition (e.g., Purves & Law 2002) to long-distance dispersal and biogeographical considerations (Whittaker et al. 2001). Observation tools vary along this range of scale as well, from point-quadrant methods (Stampfli 1991) to remote sensing methods (Gould 2000). In the case of species interactions in plant communities, fine-scale approaches to the mechanisms of coexistence are used, usually with a resolution adapted to the organism size (Gigon & Leutert 1996, Nordbakken 2000, Roxburgh et al. 2004).

Facilitation has been considered as an important mechanism explaining species coexistence (e.g., Bertness & Callaway 1994). In recent investigations, both descriptive and experimental approaches are commonly used, and the resolution at which observations are made varies from 15 cm (Tirado & Pugnaire 2005) to 4 m (Riginos et al. 2005). Meanwhile, the discussion about scale dependency of facilitation remains scarce. However, facilitation is generally drawn from the observation of positive association patterns together with a functional assumption, such as competition reduction.

In grazing ecology, the role of unpalatable species has been emphasized, giving rise to the concept of associational resistance (Smit et al. 2005, Smit et al. 2006, Vandenberghe 2006). In this context, the scale chosen a priori will influence the intensity and even possibly the orientation of the expected association.

To explain the facilitation process, the role of individual species balances between two non-exclusive hypothesis: (i) the facilitator role of some individual species is strictly determined by a strong functional identity, such as unpalatability due to chemical or mechanical defences against herbivory (e.g., Rebollo et al. 2005); and (ii) facilitation results from an additive effect of a common trait shared by several coexisting species which would individually not play any significant role (Béguin et al. submitted).

In the case of facilitation of tree regeneration in grazed systems, it is assumed that browsing is the major constraint affecting survival and growth of the tree species, and that the facilitator species mediates the intensity of the interaction with herbivores. This easily leads to the rule “closer is better” between protector and beneficiary species, with a threshold distance beyond which the positive effect cannot be detected. Such a distance-dependent effect is valuable for both hypotheses mentioned above, possibly with different thresholds due to the scale of the underlying processes and species size. But for plants, living too close from each other, it could have a negative effect, since resource or interference competition is more likely to occur in this case. Could the positive effect suddenly be reversed due to an excessive proximity? This would mean that a positive association stated at one scale could be nuanced or even discredited when observed at another scale, stressing out once more the determinant aspect of scale in detecting facilitation through positive associations.

Associational resistance has been invoked to explain tree sapling survival in mountain wood pastures of Switzerland through comparative (Chapter 1; Smit et al. 2005) and experimental (Smit et al. 2006, Vandenberghe 2006) studies. In this paper, using new data collected at two spatial resolutions in one of the previously studied sites, we want to test the hypothesis of a scale dependency of the positive *vs.* negative association between saplings of Norway spruce (*Picea abies* L. Karst) and the neighbouring plant species. Furthermore, scale dependency of the relationship between *Picea* saplings and functional traits of the surrounding species will be investigated using an observational approach in the field.

Methods

Study site

This study was carried out in a wood pasture of the Swiss Jura Mountains, at the Marchairuz site (Pré-aux-Veaux, Le Vaud VD, altitude 1340 m a.s.l., 6°12’E, 46°32’N), where facilitation processes on tree regeneration were previously investigated (Chapters 1 and 2, Smit et al. 2005). This pasture is seasonally grazed by a herd of 50 heifers, following a rotational ranging system: the herd grazes eight to ten days per paddock before passing to the next. Norway spruce (*Picea abies*) is the only dominant tree species, patchily distributed in space and present in a wide range of sizes. The geomorphological variability is high, with abundant calcareous outcrops generating a microtopography of hummocks and hollows. In this site, we selected an area of one hectare with a tree cover of 30% (see Chapter 1 for a more detailed site description).

Data collection

The field work was carried out during the vegetation period between August 2002 and July 2003. From a preliminary survey of 600 square plots of 1m^2 regularly distributed over the entire 1-hectare study area, 71 plots were randomly selected in a stratified way, covering the following situations: (i) hosting at least one spruce sapling whose height ranged between 5 and 40 cm (n = 21); (ii) hosting at least one spruce sapling, with the highest not exceeding 5 cm (n = 21); (iii) hosting no spruce saplings (n = 29).

Each 1-m^2 plot was subdivided into a regular grid of 10 by 10 cells. In every plot hosting only one spruce sapling, the 1-dm^2 cell occupied by the sapling was selected for fine scale sampling (P1C1 type). Additionally, one empty cell was randomly selected in the same plot (P1C0 type). In the plots hosting two saplings, both cells occupied by the saplings were selected as P1C1, and two empty plots were additionally selected randomly in the same plot as P1C0. Inside each plot without any spruce sapling, two empty cells were randomly selected (P0C0 type). For all random selections of the cells, a minimal distance of 10 cm was imposed between sample cells to limit spatial autocorrelation. At the end of this sampling process, 50 1-dm^2 cells with a spruce sapling and 116 1-dm^2 empty cells were selected for further investigations.

In every plot and in every selected cell, the vegetation of the herb layer was recorded as a species list.

Environmental descriptors were collected in each 1-m^2 plot, covering soil conditions and microtopography. The microtopographical position, related to the snow persistence during the early vegetation phase, was described on a three-level scale (-1 = concave; 0 = flat; 1 = convex). Slope was measured with a precision of 10%. The mean depth from the ground level to the limestone rock substrate (further called 'mean soil depth') was calculated as the average of nine measures made with a metal stick on a regular 50-cm grid. The mean soil water pH was derived from the measure of two samples using a standard method (Anderson & Ingram 1993). The same environmental descriptors were collected as the cell scale, but the soil depth and the soil water pH were measured once at the centre of each 1-dm^2 cell.

Data analysis

In each binary vegetation dataset (at plot scale and at cell scale), rare and very common species, respectively species with a frequency below 10% or above 90% were removed prior to statistical analyses.

The co-occurrence of spruce saplings with the other plant species was measured separately for plots and cells by an hypergeometric variant u_{hyp} of Bruelheide's fidelity measure u (Bruelheide 2000), proposed by Chytry et al. (2002). As a symmetric fidelity index, u_{hyp} measures the reciprocal fidelity of a given species to another one, and is appropriate to compare species fidelity values among datasets of different size (Chytry et al. 2002). If a species co-occur with spruce saplings more often than expected by assuming an independent distribution, u_{hyp} will be positive and will indicate some degree of joint fidelity of this species to the spruce saplings and of the spruce saplings to this species (Juhàsz-Nagy 1964, Chytry et al. 2002). If the two species occur independently, the hypergeometric distribution of u_{hyp} can be approximated by a normal distribution. In this case, the probability that a normally distributed random variable will take a value above 1.96 standard deviations from the mean is less than 5%. As a consequence, values of $|u_{hyp}| > 1.96$ are statistically significant at $p < 0.05$ (Chytry et al. 2002). This allows using this as a criterion to identify the species with a significant positive or negative association with spruce saplings.

Table 1: Morphological plant traits compiled from literature. Trait description and data source. Foraging value (Klotz et al. 2002), coordinate value on the C-axis within the C-S-R space, further called «C-signature» (Grime 2001), vegetative spread (Klimes et al. 1997).

Traits	Attribute	Nb of taxa with attribute	Description	Data source
Foraging value	low	27	poisonous to little forage value (1-2)	Klotz et al. 2002
	high	43	little to best forage value (3-9)	
C-signature	low	17	0	Grime 2001
	medium	16	0.1667 to 0.25	
	high	37	0.3333 to 1	
Vegetative spread	low	9	none: CLOPLA1 (1, 2, 4, 12, 16-19, 100)	Klimes et al. 1997
	medium	28	< 0.1 m: CLOPLA1 (6, 7, 9, 13, 15)	
	high	33	> 0.1 m: CLOPLA1 (3, 5, 8, 10, 11, 14)	

In order to investigate the relationship between the occurrence of spruce saplings and the functional structure of the surrounding herb community, we compiled from the literature a set of plant morphological traits (Table 1). Using this synthetic information to describe the plant community enhances our ability to interpret at each scale the functional identity of species assemblages and to identify the possible underlying processes. This was done using nonparametric rank tests to compare the u_{hyp} fidelity values of the species grouped in the functional categories presented in Table 1. Separately for each morphological trait, an overall Kruskal-Wallis rank sum test (Sokal & Rohlf 1995) was first applied. In the case of significant results, further unpaired Wilcoxon signed rank tests for plot or cell type comparison. An additional Principal Component Analysis (PCA) was achieved for the species recorded at plot scale on their morphological traits, in order to display their possible co-variations.

Fidelity indexes, nonparametric rank tests and PCA were computed with the software R 2.4.0 (R Development Core Team 2006).

Results

Picea saplings, environmental descriptors and mean cover of the plant functional groups for each plot category are presented in Table 2. Significant fidelity values u_{hyp} are presented in decreasing order for each scale in Table 3. Species u_{hyp} fidelity to spruce saplings varied from -3.28 to 3.93 at the plot scale, from -2.33 to 3.60 at the cell scale. *Linum catharticum*, *Acinos alpinus* and *Potentilla crantzii* were at strongest positively associated to spruce saplings at the meter scale, whereas the most negatively associated species were *Trifolium repens*, *Cerastium fontanum* and *Achillea millefolium*. At the decimetre scale, *Carex montana*, *Hippocrepis comosa* and *Aquilegia atrata* were the most positively associated to spruce, whereas the most negatively associated species were *Agrostis capillaris* and *Plantago atrata*.

Table 2: Picea regeneration success (sapling occurrence), environmental variables, vegetation structure and plant traits in the two categories of plots recorded at the m^2 scale, and in the three categories of cells recorded at the m^2 scale (mean ± 1 SD for quantitative variables, number of cases for qualitative variables).

	Variables (units)		Plot scale (m-2)		Cell scale (dm-2)		
			P1	P0	P1C1	P1C0	P0C0
			n=42	n=29	n=50	n=58	n=58
Tree saplings	sapling occurrence	0	-	n=29	-	n=58	n=58
		1	n=34	-	n=50	-	-
		≥2	n=8	-	-	-	-
Environmental descriptors	microtopography	concave (-1)	n=4	n=10	n=2	n=18	n=15
		flat (0)	n=10	n=16	n=23	n=35	n=39
		convexe (1)	n=28	n=3	n=25	n=5	n=4
	slope (%)		18.0 ± 10.5	12.8 ± 9.5	26.4 ± 22.4	15.8 ± 16.2	12.8 ± 14.2
	mean soil depth (cm)		9.4 ± 4.5	14.3 ± 8.0	8.9 ± 4.4	12.1 ± 7.4	14.1 ± 10.8
	soil pH-H2O		6.59 ± 0.47	5.91 ± 0.78	6.72 ± 0.46	6.54 ± 0.61	5.91 ± 0.86
Vegetation	total moss cover (%)		11.4 ± 12.2	14.1 ± 18.9	8.9 ± 14.8	5.9 ± 14.0	4.9 ± 9.4
	species richness		40.6 ± 7.2	33.8 ± 8.8	14.1 ± 3.7	12.3 ± 4.1	11.2 ± 4.3
	total plant cover (%)		88.1 ± 13.6	87.1 ± 16.4	86.7 ± 15.3	85.9 ± 20.3	81.4 ± 22.5
Plant traits	Foraging value	low	26.0 ± 10.0	19.6 ± 15.5	28.9 ± 17.9	29.5 ± 23.5	24.1 ± 24.6
(mean cover)		high	73.8 ± 10.1	77.2 ± 21.5	71.1 ± 17.9	70.5 ± 23.5	75.9 ± 24.6
	C-signature	low	20.3 ± 10.7	14.6 ± 10.7	19.1 ± 16.3	17.4 ± 14.6	15.2 ± 18.0
		medium	23.4 ± 6.6	20.0 ± 7.9	31.9 ± 16.4	30.4 ± 20.2	27.4 ± 19.7
		high	56.1 ± 11.1	62.3 ± 15.1	49.0 ± 20.3	52.1 ± 20.5	57.4 ± 23.5
	Vegetative spread	low	6.3 ± 3.9	6.1 ± 4.1	6.6 ± 12.0	7.1 ± 9.5	10.4 ± 17.0
		medium	57.6 ± 9.8	42.4 ± 17.8	62.0 ± 17.1	59.1 ± 25.3	46.5 ± 25.2
		high	35.8 ± 10.5	48.4 ± 17.1	31.4 ± 16.9	33.8 ± 24.2	43.2 ± 26.5

Table 3: Species positively or negatively associated with Picea saplings according to the hypergeometric fidelity index u_{hyp} (decreasing order). Species with a frequency below 10% or above 90% have been removed.

Plot scale (m^2) **n=72**			
	fidelity	frequency	mean cover
positively associated with Picea saplings			
Linum catharticum	3.93	0.542	0.2%
Acinos alpinus	3.83	0.597	1.0%
Potentilla crantzii	3.57	0.847	3.7%
Hippocrepis comosa	3.56	0.750	4.0%
Anthyllis alpestris	3.53	0.722	1.2%
Aster bellidiastrum	3.31	0.625	1.6%
Aquilegia atrata	3.28	0.653	1.4%
Leucanthemum vulgare	3.08	0.611	1.5%
Daphne cneorum	2.82	0.625	3.6%
Polygala alpestris	2.74	0.458	0.2%
Carduus defloratus	2.65	0.583	2.0%
Campanula rotundifolia	2.55	0.639	0.2%
Carex sempervirens	2.52	0.667	5.3%
Alchemilla conjuncta	2.47	0.778	5.1%
Gymnadenia conopsea	2.47	0.25	0.4%
Campanula thyrsoides	2.36	0.153	2.2%
Thymus pulegioides	2.33	0.875	3.4%
Senecio integerifolius	2.30	0.278	0.5%
Euphorbia brittingeri	2.20	0.736	2.2%
Sanguisorba minor	2.17	0.583	3.7%
Carex flacca	2.11	0.611	1.8%
Gentiana campestris	2.11	0.181	0.3%
Euphrasia montana	2.06	0.639	0.5%
negatively associated with Picea saplings			
Trifolium repens	-2.17	0.583	1.6%
Cerastium fontanum	-2.21	0.181	0.2%
Achillea millefolium	-2.25	0.153	2.0%
Nardus stricta	-2.49	0.306	6.5%
Veronica officinalis	-3.28	0.264	1.5%

Cell scale (dm^2) **n=166**			
	fidelity	frequency	mean cover
positively associated with Picea saplings			
Carex montana	3.60	0.681	19.3%
Hippocrepis comosa	3.59	0.223	7.2%
Aquilegia atrata	3.45	0.139	4.8%
Anthoxanthum alpinum	3.43	0.229	3.7%
Potentilla crantzii	3.20	0.572	6.6%
Carduus defloratus	3.05	0.151	8.4%
Daphne cneorum	3.03	0.313	8.9%
Sanguisorba minor	2.80	0.398	9.7%
Galium anisophyllon	2.70	0.500	1.2%
Thymus pulegioides	2.52	0.614	4.0%
Acinos alpinus	2.51	0.169	3.4%
Homogyne alpina	1.97	0.223	9.4%
negatively associated with Picea saplings			
Agrostis capillaris	-2.27	0.392	8.8%
Plantago atrata	-2.33	0.458	5.3%

To visualize the effect of the observation scale on the association between spruce and other species, species were displayed on a scatter plot by their fidelity u_{hyp} values at plot *vs.* cell scale (Figure 1). The overall trend followed the y = x diagonal, but some species fell apart, revealing the particular scale-dependence of their fidelity to spruce. Among those, the association of *Euphorbia brittingeri* and *Gentiana campestris* to spruce were significantly positive at the plot scale and marginally negative at the cell scale. *Hieracium pilosella* and *Gentiana lutea* displayed the same opposition, but not significantly. By constrast, the association of *Plantago atrata* to spruce was significantly negative at the cell scale and positive but not significant at the plot scale (Figure 1).

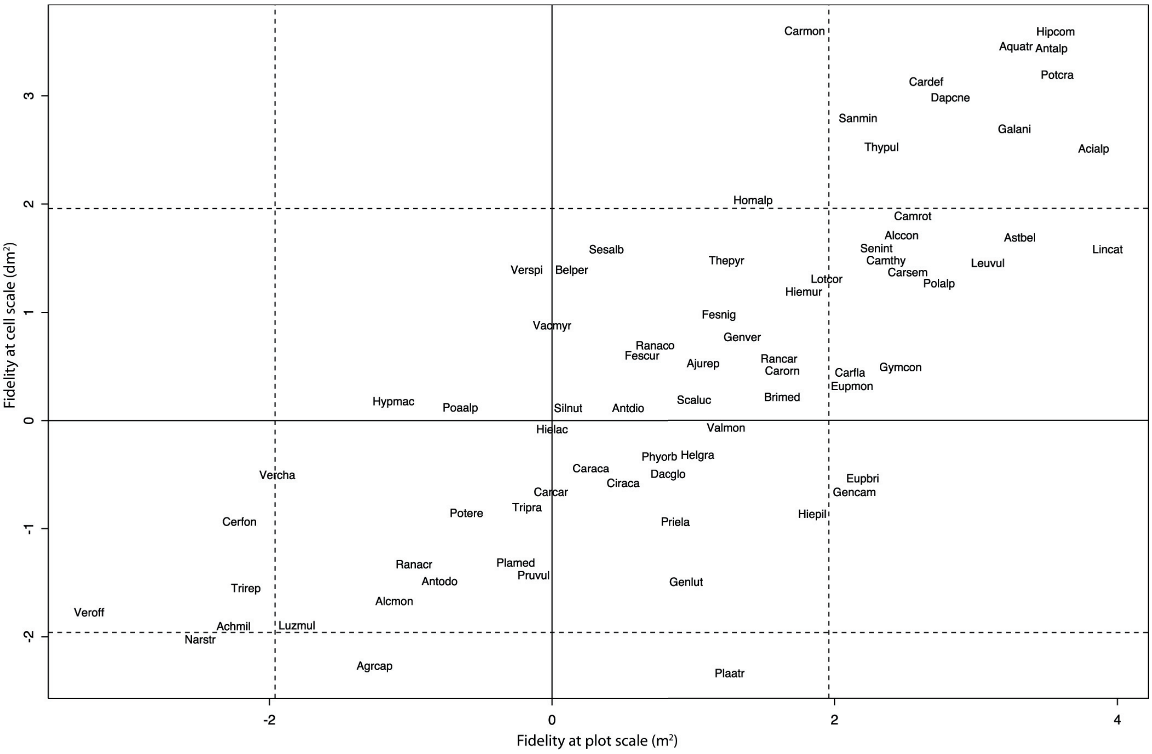

Figure 1: Scatter plot of the fidelity values u_{hyp} for the surrounding species at both scales. Fidelity values at the square meter scale are displayed on the X-axis and the fidelity values at the decimetre scale on the Y-axis. Dashed lines represent the significant level at $|u_{hyp}| > 1.96$ for both scales. Only species with frequency > 10% at m^2 scale are plotted.

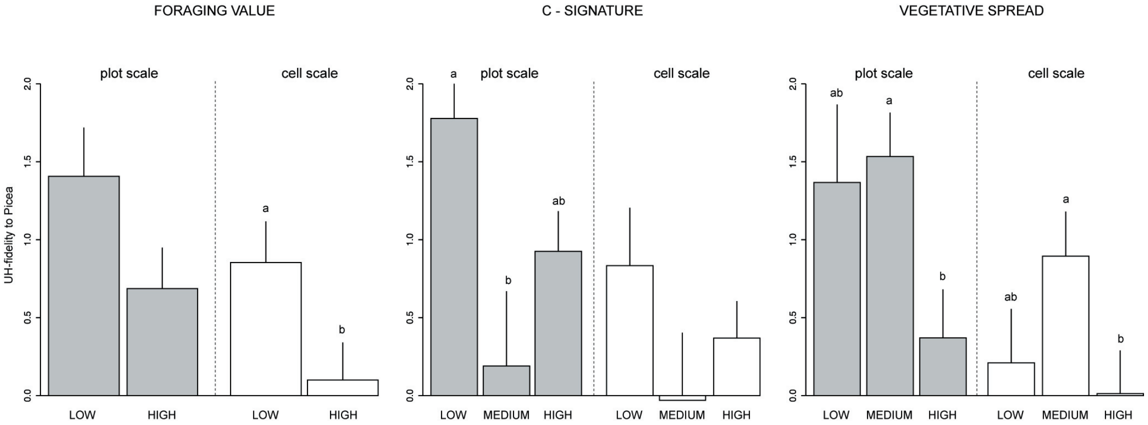

Figure 2: Fidelity values u_{hyp} of the species belonging to the different levels of the functional traits foraging value, C – signature and vegetative spread ability at both scales (mean ± 1 SD).

As far as morphological traits are concerned (Figure 2), the fidelity to spruce differ significantly between species of low and high foraging value at the cell scale only (unpaired Wilcoxon signed rank test: V-value = 754.5, *P*-value = 0.0363), the species of low foraging value displaying a higher association to saplings. For the C-S-R plant strategies, the fidelity to spruce differ significantly between medium and week competitors at the plot scale only (unpaired Wilcoxon signed rank test: V-value = 209.5, *P*-value = 0.0085), week competitors (i.e. species with a low C-signature) showing a higher association to saplings. Finally, the fidelity to spruce differ significantly between species with a medium or a high ability for vegetative lateral spread, both at the plot scale (unpaired Wilcoxon signed rank test: V-value = 663, *P*-value = 0.0136) and at the cell scale (unpaired Wilcoxon signed rank test: V-value = 607.5, *P*-value = 0.0358), species that strongly spread through vegetative growth displaying the lowest fidelity to saplings. Last, the PCA analysis of functional traits showed that ability for vegetative spread and C-signature mainly structured our vegetation species pool, whereas fewer differentiations appeared for the foraging value of species (Figure 3).

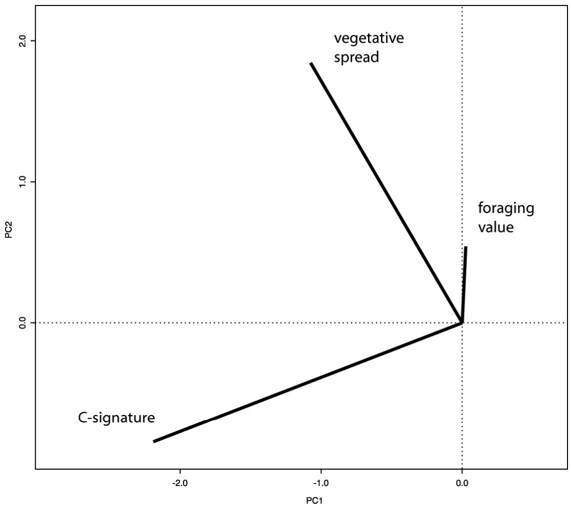

Figure 3: Scatter plot of the PCA of plant functional traits recorded at the m^2 scale. Displayed variation: axis 1: 50.3%, axis 2: 33.8%. Total inertia: 1.513.

Discussion

Individual plant species

Looking at individual plant species and their fidelity to spruce saplings, it turns out that the number of species with a significant positive or negative association with spruce is lower at the dm^2 scale compared to the m^2 scale. This indirect effect of scale can be attributed to the two different sizes of the sampling units. Decreasing the size of the observation unit is likely to increase the chance to get particular conditions, especially while being in our case far below the “minimal area” generally considered for such a grassland community (about 20 m^2). Moreover, the presence or absence of one single species has more weight in the description of the assemblage at the dm^2 scale, due to space limitation. To compensate at least part of this sampling effect, we deliberately chose a higher number of samples at the finer scale.

Among the pool of species observed in the landscape, some of them show a significant positive association with spruce saplings at both scales, e.g., *Hippocrepis comosa*, *Potentilla crantzii*, *Sanguisorba minor*, *Thymus pulegioides* and *Acinos alpinus*. These species being themselves frequently associated together, they could draw the outlines of a possible plant community which could be favourable as a whole for the establishment of spruce. Three other species were positively associated with spruce saplings at both scales: *Aquilegia atrata*, *Carduus defloratus* and *Daphne cneorum*. Morphology and current knowledge about these three species let us suspect them to play in our system the role of possible facilitator species due to their low palatability: *Aquilegia* is known to be a toxic plant, whereas *Carduus defloratus* is partly avoided by cattle because of its spines. Finally, *Daphne cneorum*, a rare but locally abundant creeping shrub is mostly not grazed.

At the m^2 scale, many other species were positively associated to spruce saplings as well, most of them being frequent but not dominant at this scale, such as *Linum catharticum*, *Anthyllis vulneraria* subsp. *alpestris*, *Aster bellidiastrum*, *Leucanthemum vulgare* and *Polygala alpestris*. These species might belong at least partly to the same community raised around the set of species positively associated to spruce at both scales, for sure driven partly by similar ecological requirements, without any evidence for a direct facilitator effect on tree regeneration. The fact that part of these did not show up significantly at the finer scale might possibly be explained by their low average cover, reducing their frequency in smaller sampling units.

At the dm^2 scale, the highest fidelity to spruce saplings was observed for *Carex montana*. Thanks to its high vegetative spread and its tolerance to stress, this frequent species grows usually in small dense patches. It did not appear significantly associated to spruce at the coarser scale, revealing a possible strong local effect specific to the finest scale and which could not be detected with a resolution of one meter.

Only few species showed a significant negative association with spruce ($u_{hyp} < -1.96$). Among those, we found at the plot scale a set of species with a potentially high competitive growth ability. In particular, *Trifolium repens*, *Nardus stricta* are strong competitors in suitable conditions, forming large dense patches in which spruce saplings can hardly establish. Furthermore, *Trifolium repens*, *Achillea millefolium* and *Veronica officinalis* can rapidly colonize canopy gaps in productive grasslands (Kohler et al. 2006), preventing spruce sapling emergence through competitive exclusion.

Beside the dominant trend of species with more or less similar fidelity to spruce at both scales, it is interesting to notice that the fidelity of some species showed a high sensitivity to scale, by showing a positive association at coarse scale but a negative or neutral association at fine scale (Figure 1). Among those, three are suspected to be potentially strong facilitator species, due to their unpalatability: *Gentiana lutea*, *Euphorbia brittingeri* and *Hypericum maculatum*. Even if these differences have to be confirmed, this should warn us from early conclusions on their potentially important role as facilitator species in the natural context of pasture woodlands, and highlight us the fact that the scale of description will determine the conclusion we might get out of patterns (Purves & Law 2002). These authors showed in particular that two species (*Agrostis stolonifera* and *Lolium perenne*) can be segregated at the smaller scale (4 cm^2) and meanwhile seen as aggregated at the larger scale (64 cm^2).

The high variability of the association degree of potentially true facilitator species compared to “banal” species constituting the biggest part of community assemblages relative to scale let us suppose that the role of facilitation is overestimated as a general process explaining tree regeneration in our system. As direct interactions between herbaceous species are more likely to occur between species occupying the same dm^2 compared to species in the same m^2, suspected direct interactions should be searched at the dm^2 scale. However, this does not exclude the possible distant effect of unpalatable species, mediated for example by the activity of herbivores. Could these indirect effects still be considered as species-species interactions? And therefore still as facilitation, which suppose to be a direct interaction? Our results support the alternative hypothesis of patterns resulting only partly from positive associations due to indirect facilitation (Levine 1999, Pagès et al. 2003), where species with a specific unpalatability due to spines or toxicity only play a minor role.

Functional traits

Considerations on the role of individual species on tree regeneration lead us naturally to the alternative approach, where the plant community is not described anymore as a set of coexisting species, but as the assemblage of a reduced number of functional types, generally derived from species characteristics (Table 1). This might bring us a bit closer to possible underlying processes acting in this complex system.

In our case, vegetative spread was a common trait among plant species (Table 1). 27 of the 70 observed plant species were considered to be of low foraging value, most of them being forbs (20 species; see Table 1).

Our results suggest that fidelity of surrounding species to spruce saplings depends on their foraging value only at the dm^2 scale, which is approximately the scale of the selective grazing behaviour of a cow. At this scale, we can suspect the selectivity of grazing to happen, the cow being particularly interested in species of high foraging value. As a consequence, species of low foraging value are likely to remain mostly untouched. Therefore, some of these species (e.g., *Acinos alpinus*, *Potentilla crantzii*, *Hippocrepis comosa*) will appear to be positively associated with spruce saplings at the dm^2 scale. Additionally, few other species of low foraging value were associated positively with spruce saplings at the plot scale but not at the cell scale (e.g., *Euphorbia brittingeri*, *Gentiana campestris*).

Our results also suggest that two potential scenarios related to C-S-R plant traits might happen simultaneously: (i) species with a low competitive ability remain tolerable neighbours for spruce saplings as they are not able to compete much for light and space, allowing the coexistence with saplings; (ii) species with a high competitive ability and low foraging value (50 % of the species with high C-signature) may reduce the visual attractiveness of the patch for large herbivores mostly at a m^2 scale, without necessarily affecting saplings by direct competition at this scale.

According to our results, species with a high vegetative spread ability were less associated to spruce saplings compared to species with a moderate vegetative spread ability. As vegetative spread ability often relates to a way of competitive exclusion for other species, spruce saplings might be affected by competition when surrounded by species with a high clonal reproduction. On the other hand, species with a low vegetative spread ability are mostly species with a low foraging value (77.8 %). Their low palatability and the low competitive pressure they have on surrounding plants due to their growth form could explain why such species were frequently associated with spruce saplings, especially at the m^2 scale.

Globally, it appears that functional traits related to palatability and competition ability show up as pertinent characteristics of the plant community surrounding tree saplings in discussing how it might drive tree regeneration. The interplay between local plant communities and tree recruitment rehabilitates the possible role of the overall set of species, besides the role of a few functionally well-defined facilitator species. It might be seen as easy to step in functional considerations from species traits from which we suppose a functional effect. But taking the question from one a priori function itself, it gets harder to match species to such given functions, as these might vary depending on scale and context as we show for facilitation.

The nature of spatial structure appears to depend on the scale of observation. According to Purves & Law (2002), smaller-scale data are more likely to provide a biologically interpretable measure of local spatial structure in this community. Our conclusions confirm that the use of a single spatial scale of inquiry can potentially misrepresent the importance of a particular interaction, such as competition or facilitation, as Lortie et al. (2005) have recently argued. In this context, we support the caution of these authors about results of experiments on simplified systems, pointing out the challenge experimental scientists have to face: the patterns and final net effects within a real community might be quite different than those predicted from experimental results.

The problem of scaling up keystone effects from simple to complex ecological networks was raised by Brose et al. (2005). In this sense, any evidence of a species-species interaction such as facilitation in a simplified experimental system does not imply that this relationship operates in a natural community where complex hierarchical interactions take place.

Acknowledgements

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Appendix 1 – abbreviation list of plant species used in the figures.

Achmil = *Achillea millefolium*; Acialp = *Acinos alpinus*; Agrcap = *Agrostis capillaris*; Ajurep = *Ajuga reptans*; Alccon = *Alchemilla conjuncta*; Alcmon = *Alchemilla monticola*; Antalp = *Anthyllis vulneraria* subsp. *alpestris*; Antdio = *Antennaria dioica*; Antodo = *Anthoxanthum odoratum*; Aquatr = *Aquilegia atrata*; Astbel = *Aster bellidiastrum*; Belper = *Bellis perennis*; Brimed = *Briza media*; Camrot = *Campanula rotundifolia*; Camthy = *Campanula thyrsoides*; Caraca = *Carlina acaulis*; Carcar = *Carum carvi*; Cardef = *Carduus* *defloratus*; Carfla = *Carex flacca*; Carmon = *Carex montana*; Carorn = Carex ornithopoda; Carsem = *Carex sempervirens*; Cerfon = *Cerastium fontanum* subsp. *triviale*; Ciraca = *Cirsium acaule*; Dacglo = *Dactylis glomerata*; Dapcne = *Daphne cneorum*; Erialp = *Erigeron alpinus*; Eupbri = *Euphorbia brittingeri*; Eupmon = *Euphrasia roskoviana* subsp. *montana*; Fesnig = *Festuca nigrescens*; Fesovi = *Festuca curvula*; Galani = *Galium anisophyllon*; Gencam = *Gentianella campestris*; Genlut = *Gentiana lutea*; Genver = *Gentiana verna*; Gymcon = *Gymnadenia conopsea*; Helnum = *Helianthemum nummularium* subsp. *grandiflorum*; Hielac = *Hieracium lactucella*; Hiemur = *Hieracium murorum*; Hiepil = *Hieracium pilosella*; Hipcom = *Hippocrepis comosa*; Homalp = *Homogyne alpina*; Hypmac = *Hypericum maculatum*; Leuvul = *Leucanthemum vulgare*; Lincat = *Linum catharticum*; Lotcor = *Lotus corniculatus*; Luzmul = *Luzula multiflora*; Narstr = *Nardus stricta*; Phyorb = *Phyteuma orbiculare*; Plaatr = *Plantago atrata*; Plamed = *Plantago media*; Poaalp = *Poa alpina*; Polalp = *Polygala alpestris*; Potcra = *Potentilla crantzii*; Potere = *Potentilla erecta*; Priver = *Primula veris*; Pruvul = *Prunella vulgaris*; Ranaco = *Ranunculus aconitifolius*; Ranacr = *Ranunculus acris* subsp. *friesianus*; Rancar = *Ranunculus carinthiacus*; Sanmin = *Sanguisorba minor*; Scaluc = *Scabiosa lucida*; Sescae = *Sesleria albicans*; Silnut = *Silene nutans*; Thepyr = *Thesium pyrenaicum*; Thypul = *Thymus pulegioides*; Tripra = *Trifolium pratense*; Trirep = *Trifolium repens*; Vacmyr = *Vaccinium myrtillus*; Valmon = *Valeriana montana*; Vercha = *Veronica chamaedrys*; Veroff = *Veronica officinalis*; Verspi = *Veronica spicata*.

CHAPTER 4

Spatial patterns of saplings and trees in *Picea*-dominated wood pastures

Introduction

Present landscape patterns reveal much about past processes and land use (Lindborg & Eriksson 2004, Peterson 2002). For man-made landscapes, they result from the interdependence of natural and cultural processes shaping over time and space complex and often highly structured landscapes (Bolliger et al. 2003, de Blois et al. 2001, de Blois et al. 2002). Beside the cultural heritage they represent, traditional landscapes often constitute examples where multifunctional purposes can be found within one single ecosystem (Fuhlendorf & Engle 2004, Mottet et al. 2006). Such coexisting vocations, as agricultural and pastoral land use, or forestry exploitation generate unique ecological niches often coexisting in a very dynamical way (Ericsson et al. 2000, Fraterrigo et al. 2006, Yeo & Blackstock 2002). According to the intermediate disturbance hypothesis (Roxburgh et al. 2004), intermediate disturbance levels due to agricultural practices and natural events generate spatial and functional complexity hosting high levels of species diversity. Although, these ecosystems are often in an unstable equilibrium, the intensification of one particular practice generally weaken the equilibrium of niche coexistence, meaning a loss of diversity in habitats and species (Cousins et al. 2003, Ericsson et al. 2000, Tilman 1999). Finally, such semi-natural ecosystems can be considered as models of sustainable resource management where natural and economical values are taken into account in a process-based landscape management (Benton et al. 2003, Blaschke et al. 1992, Mottet et al. 2006).

As remaining of traditional semi-natural ecosystems in Central Europe, wooded pastures recently raised as a model system motivating many recent studies in ecology (Gillet et al. 2002, Gillet 1996, Kohler et al. 2006, Vandenberghe et al. 2007). As structural species, trees play an important role and their regeneration has been shown to be a key process driving further patterns of species and habitat types (Dzwonko & Loster 1997, Gillet et al. 1999), as well as further processes such as cattle behaviour or species dispersal (e.g., Werth et al. 2006). In such ecosystems living on disturbance, the spatial associations between adult trees and saplings of the growing tree cohort provides a precious outlook on the spatio-temporal dynamics of the forest subsystem and its stability over time.

Observed patterns of seedling distribution result from the interaction between seed dispersal and habitat-specific seedling response to environmental variation. Under harsh conditions as could be found at lower tree lines or in semiarid environment, self-enhancing feedback mechanisms of adult trees on seedlings stabilize the woodland-grassland ecotones both spatially and temporally due to natural shading effect on seedling recruitment (e.g., Bellot et al. 2002, Vetaas 1992, Weltzin & McPherson 1999). On the other hand, the neighbourhood with a higher tree may suppress the individual growth and survival of saplings, probably through above and below-ground competition (e.g., Dolezal et al. 2006). In both cases, spatial associations reveal something about the ecological underlying processes driving tree recruitment and growth under constrained conditions.

Beside the initial liming factor of seed dispersal, abiogenic environmental conditions (climate, soil, geology) and disturbance often constrain much of the spatial distribution and species composition of tree recruitment cohorts (Weltzin & McPherson 1999). Occasional forest fire (Arseneault 2001, Kuuluvainen & Rouvinen 2000), tree fall and windthrow (Grau 2002, Ilisson et al. 2006) or pests (Orwig & Foster 1998) will offer specific environmental conditions determining specifically composition and structure of forest patches. Browsing by wild or domestic animals (Jefferies et al. 1994, Weisberg & Bugmann 2003) will contribute as well in maintaining continuous favourable conditions for a dynamical tree community, allowing the maintenance of pioneer species over time (Engelmark et al. 1998). Finally, neighbouring plant communities and specific species such as shrub species constitute either protective structures (Miriti 2006) or competitive neighbours (Gorchov & Trisel 2003) determining as well tree recruitment patterns.

In wood pastures, nurse structures such as shrubs or unpalatable herbaceous plant species has been shown to prevent tree saplings from cattle browsing (Chapter 1, Smit et al. 2005, Smit et al. 2006). These positive associations have been investigated at fine scale and partly through experimental approaches and, we see now the necessity to come back to a larger scale at which management choices are mostly operating (Gillet 1996). Pattern analysis on overall species distribution and cattle behaviour were carried out recently at the management unit scale (Dufour et al. 2006, Kohler et al. 2006), but forest aspects received less attention yet.

Our previous studies showed the importance of the surrounding plant communities, offering at specific scales suitable conditions for the recruitment of *Picea abies* in wood pastures, in addition to edaphic and light conditions. Spatial association between tree sapling distribution and adult trees remained as an untouched aspect yet, as outcome and synthesis at the landscape scale of underlying processes over the long term. In order to investigate this further on, a descriptive study was carried out in two contrasted wood pastures of the Swiss Jura, in order to explore the following hypotheses: (i) presence and abundance of shrubs enhance the recruitment of tree species under grazed conditions; (ii) neighbouring trees can play the role of facilitative structures for tree saplings, in particular when no other nurse structure offers protection against cattle browsing. More generally, it will contribute in answering the general question of what the current spatial pattern of trees can tell us about the major processes driving past and present tree recruitment and growth in the pasture woodland context. Finally, an allometric growth model was established to provide a tool and a temporal outcome for further modelling perspectives on tree recruitment and growth in such a context.

Methods

Study site

This study was conducted in two wooded pastures, about 73 km apart, lying in the central part of the Swiss Jura Mountains where previous studies on tree recruitment were achieved. In both sites, the climate is continental, with Atlantic influences bringing depressions from the West. Mean yearly temperature varies between 3° and 5° C. Although annual precipitation is between 1400 and 2000 mm (with peaks in summer) the soils are considered relatively dry because of the high permeability of the underlying calcareous layers (Gallandat et al. 1995). In combination with low winter temperature, this leads to a relatively short growing season of approximately four months. Every year, the ground is covered by snow during about 120 days between November and April.

The landscape is very heterogeneous with large geomorphological and geological variations. This influences vegetation patterns, with closed forest patches being mainly associated with rock outcrops and steep slopes, pastures and wooded pastures with flat surfaces or gentle slopes where the soils are more favourable for agriculture. Norway spruce (*Picea abies*) is the naturally dominant tree species, occurring as isolated individuals or in small groups in open grasslands. Other tree species, like maple (*Acer pseudoplatanus*), white fir (*Abies alba*) and beech (*Fagus sylvatica*), do occur in the surrounding ungrazed forests beside Norway spruce, but are rarely found in the pastured areas.

Two grazing systems are commonly applied on these seasonal pastures: ‘rotation-grazing’ where pastures are divided in paddocks and animals pass from one paddock to another according to a variable period of rotation and ‘free ranging’ where animals spend the whole grazing season roaming freely through unpartitioned pastures (Gillet & Gallandat 1996). Beside the pastoral activity, occasional tree harvesting for burning wood occurs in both sites, usually done by the owners themselves, under the governance of the local forest officer.

The Marchairuz site (Pré-aux-Veaux, Le Vaud VD, altitude 1340 m a.s.l., 6°12’E, 46°32’N) is divided into seven roughly even sized paddocks, which are grazed in turn (rotation system); our selected paddock measured ca 15 hectares. The herd (82 Adult Bovine Units day ha^{-1}) grazes eight to ten days per paddock before passing to the next. On the other hand, the La Sagne site (Communal, La Sagne NE, altitude 1150 m a.s.l., 6°48’E, 47°02’N) is grazed by free ranging cattle (50 ABU day ha^{-1}). In each site, we selected a surface of 0.99 hectare (90 m x 110 m) having a tree cover of 30% in the Marchairuz site and 40% in La Sagne site, both dominated by *Picea abies*.

Data collection

The field work was carried out between July and September 2004 in the Marchairuz site and between August and September 2005 in La Sagne site.

In each surface of 0.99 hectare, reference points were set and permanently marked at the nods of a regular 10 m x 10 m cell grid. From these reference points, the position of every tree over 1.5 m height was recorded using distance measures along the two axes of the overall grid. Furthermore, for each tree, the following data were collected: (i) the species; (ii) the mean stem diameter at 1.3 m above ground level (further called DBH for diameter at breast height), taken from two perpendicular measures done to the nearest

0.5 cm along and transversal to the slope; (iii) the tree height from the ground measured with a inclinometer; (iv) the mean crown radius taken from two perpendicular measures along and transversal to the slope.

The following descriptors on the shrub layer and recruiting trees below 1.5 meter height were collected for each 5 m x 5 m cell set within the 10 m x10 m grid of reference points: (i) visual cover estimation of shrubs using ranges of values (0%, 1%, 2%, 3%, 4%, 5%, 5-15%, 15-25%, 25-50%, 50-75%, 75-100%); and (ii) species and amount of tree saplings between 0.4 and 1.5 m height.

Data analysis

Most height-DBH functions modelling tree allometry are nonlinear models (Huang et al. 1992). Unlike other species, some *Picea* species are best described by linear models, when the height development is apparently not asymptotic (Smith & Watts 1987). Therefore, a linear model of the log-transformed tree height was built on log-transformed DBH values, for both sites together. The significance of the model components was tested using an analysis of variance (ANOVA) after preliminary check for normality of the deviations using a normal Q-Q plot of the observed residuals, and a plot of fitted values against the residuals.

In order to have consistent data on the 5 m x 5 m cell grid, the tree canopy cover in each cell was computed from the X-Y coordinates and the average crown radius of each tree, using an ArcGIS (ESRI Corp.) procedure generating trees as circles of average crown radius and calculating the surface intersections between the cell grid and this ensemble of circles. For shrub cover, the median value of ranges of values was taken for further calculations. Shrub cover, tree cover and the amount of *Picea* saplings were displayed to identify possible spatial structures.

Correlations between tree cover, shrub cover and *Picea* sapling number were estimated using Spearman's coefficient, the significance tests for rank correlations corrected using the procedure of Dutilleul (1993) implemented in the Mod_t_test program (Legendre & Gallagher 2001) to account for spatial autocorrelation.

In order to assess the relative importance of spatial structures of different scales in the observed tree pattern and have an outlook on the scale of possible processes generating such a structure, we performed multiple linear regressions on the tree cover. A spatial explanatory variable was constructed with the principal coordinates of neighbour matrices method (PCNM) (Borcard & Legendre 2002). This method uses eigenvectors of a principal coordinate analysis (PCoA) of a truncated matrix of geographical distance among cells as spatial descriptors and allows to detect patterns at a wide range of scales. 208 PCNMs were calculated, the highest unmodified distance value was given at 10 meters. To avoid overfitting in the multiple linear regression model, we performed a selection of PCNMs using the stepAIC procedure based on the Akaike's Information Criterion (Akaike 1973). At each stage of the model selection, the current model was modified by adding or removing a single PCNM until the model could not be improved. Only significant PCNMs at the *P*-value < 0.001 were retained.

PCNMs were calculated with the Spacemaker2 program (Borcard & Legendre 2004), whereas linear and multiple linear regressions, as well as the stepwise model selection procedure were performed with R 2.4.0 (R Development Core Team 2006).

Results

In the Marchairuz site, 258 saplings (up to 1.5 m high) of three species were recorded. *Picea abies* was the most abundant with 249 individuals whereas *Acer pseudoplatanus* and *Sorbus aucuparia* were represented by 2 and 7 individuals respectively (Table 1). Furthermore, 270 trees (above 1.5 m high) were recorded and measured, *Picea abies* being also numerous with 258 individuals, beside one *Abies alba* tree and a few *Salix* and *Sorbus* trees (Table 1).

Table 1: Species, number, height, stem diameter at 1.3 meters above ground level (DBH) and crown radius on saplings below 1.5 meters high and trees above 1.5 meters high in the Marchairuz and La Sagne sites (sampling surface: 0.99 hectare).

		number	height (m)	DBH (cm)	crown radius (m)
		Marchairuz site			
Saplings ≤ 1.5 meter high					
	Acer pseudoplatanus	2	0.80 ± 0.29	nm	0.28 ± 0.04
	Picea abies	249	0.98 ± 0.29	nm	0.52 ± 0.19
	Sorbus aucuparia	7	1.22 ± 0.18	nm	0.19 ± 0.08
Trees > 1.5 meter high					
	Abies alba	1	3.90	3.0	1.45
	Picea abies	258	6.34 ± 6.27	12.6 ± 15.5	1.60 ± 0.99
	Salix caprea	2	2.00 ± 0.63	nm	0.63 ± 0.11
	Sorbus aria	3	2.17 ± 0.43	nm	0.90 ± 0.48
	Sorbus aucuparia	6	5.05 ± 2.24	10.8 ± 5.9	1.68 ± 0.54
		La Sagne site			
Saplings ≤ 1.5 meter high					
	Abies alba	1	nm	nm	nm
	Acer pseudoplatanus	22	nm	nm	nm
	Fagus sylvatica	12	nm	nm	nm
	Picea abies	140	nm	nm	nm
	Salix caprea	19	nm	nm	nm
	Sorbus aucuparia	24	nm	nm	nm
Trees > 1.5 meter high					
	Abies alba	3	10.93 ± 7.16	28.2 ± 20.3	2.95 ± 1.74
	Acer pseudoplatanus	13	9.73 ± 4.16	12.6 ± 9.3	2.37 ± 1.19
	Fagus sylvatica	8	10.94 ± 5.90	14.3 ± 10.4	2.77 ± 1.81
	Picea abies	285	11.36 ± 8.00	20.9 ± 17.3	2.23 ± 1.27
	Sorbus aria	7	7.83 ± 5.18	12.1 ± 10.9	2.03 ± 1.27
	Sorbus aucuparia	39	6.43 ± 3.17	6.2 ± 3.4	1.25 ± 0.61

At the La Sagne site, 218 saplings of six species were recorded. With 140 saplings, *Picea abies* was also the most abundant species, but *Acer pseudoplatanus* (n = 22), *Sorbus aucuparia* (n = 24), *Salix caprea* (n = 19) and *Fagus sylvatica* (n = 12) also occurred quite often (Table 1). This reflected the diversity of the trees above 1.5 m high, where *Picea abies* was recorded 285 times, beside *Sorbus aucuparia* (n = 39), *Acer pseudoplatanus* (n = 13) and *Fagus sylvatica* (n = 8). *Sorbus aria* and *Abies alba* also occurred occasionally (Table 1).

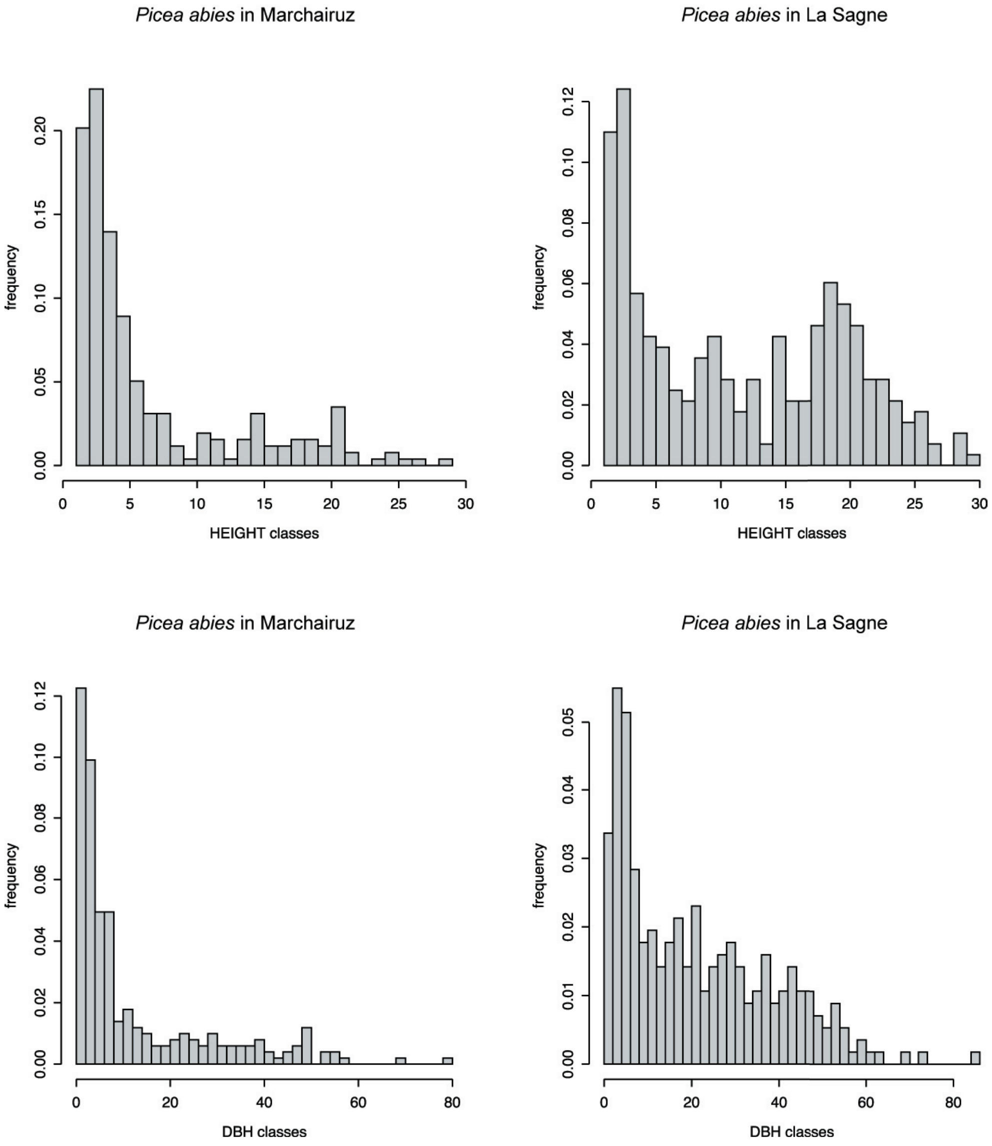

Figure 1: Height and DBH distribution of Picea abies trees in Marchairuz and La Sagne sites. Only trees above 1.5 m high were considered here.

The height distribution of *Picea* trees shows in both sites a similar shape (Figure 1). A first numerous cohort of trees below 5 m high appears, followed by a second important cohort of trees between 15 and 25 m high. In between, a hollow indicating a gap in the population size structure appears. This is even more pronounced in La Sagne site. The same shape and tendency can be seen for the DBH distributions in both sites (Figure 1), revealing a possible change in management practices affecting tree recruitment.

The display of the spatial pattern of tree cover shows a mosaic structure in both sites, being globally denser in La Sagne site (Figures 2, 3). This spatial pattern can be described as a reticulated one, interconnected forest patches structuring the space with in between few open areas. Additionally, a couple of isolated patches show up in openings, formed by an solitary tree or by a small group of trees (Figures 2, 3). In Marchairuz site, a gradient appears along both X- and Y-axes, revealing major openings of grassland areas. In the La Sagne site, openings appears as well but of smaller size.

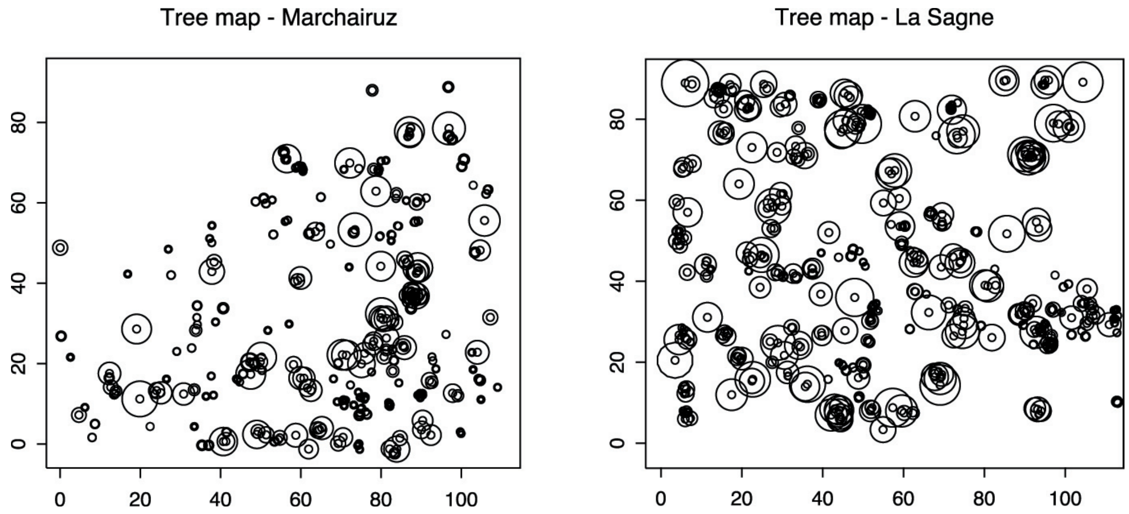

Figure 2: Maps of the trees above 1.5 m high, in both sites.

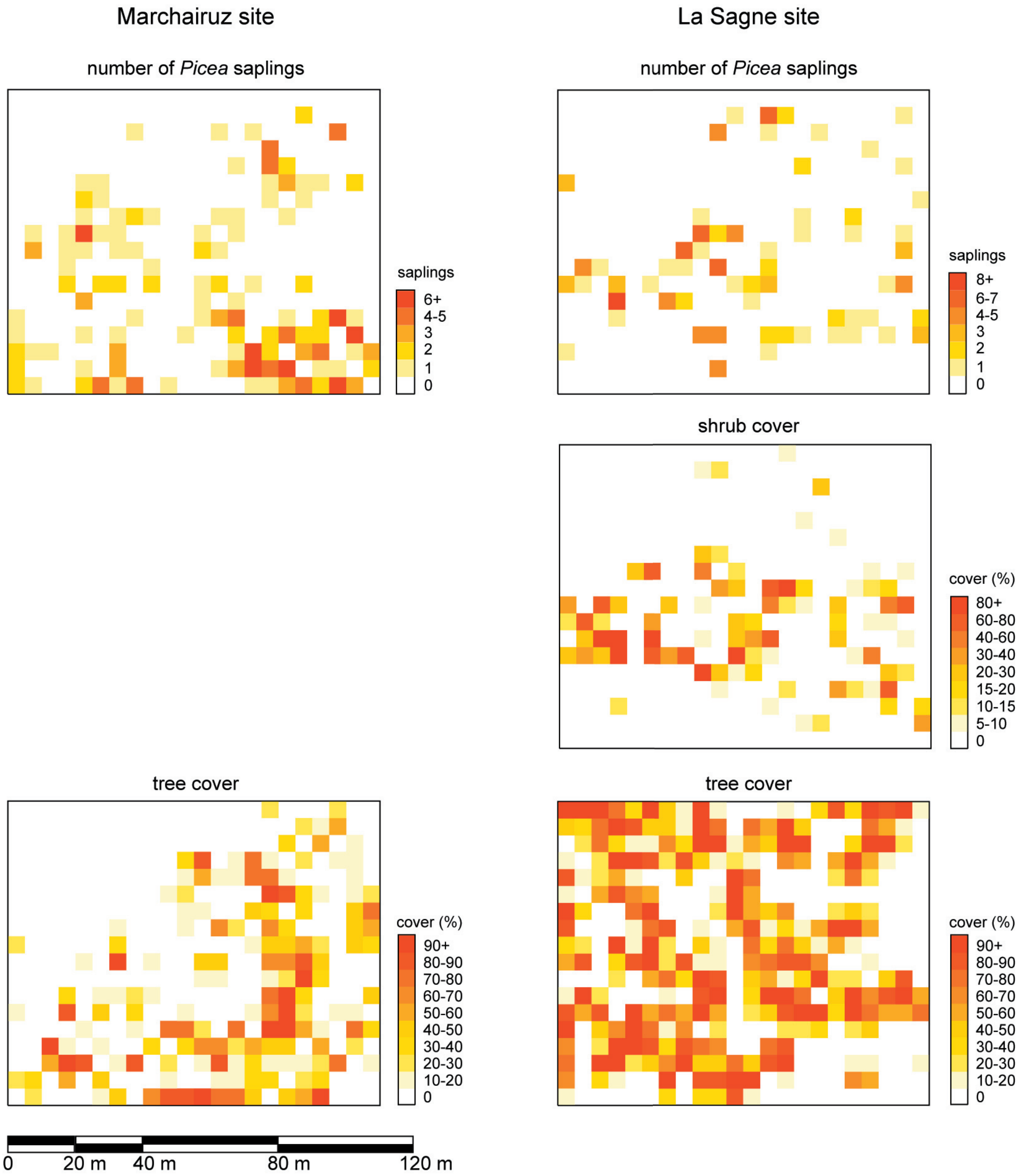

Figure 3: Maps of Picea abies sapling number, shrub cover (only La Sagne site) and tree cover in the cell grid for both sites (396 cells of 5 m x 5 m). Only comparisons among maps of the same site are meaningful.

Picea saplings are locally dense in both sites, beside other areas without any recruiting tree. Intermediate densities, in connection with higher density plots, appear to be arranged in a reticulated way as well. After accounting for spatial autocorrelation, Spearman's rank correlations reveal contrasted results between both sites (Table 2). In the Marchairuz site with no shrub cover at all in the study area, the number of *Picea* saplings is positively correlated with the tree cover (Table 2). In the La Sagne site where shrubs occurred regularly, the number of *Picea* saplings is not correlated any more with tree cover. On the other hand, *Picea* saplings appear to be positively correlated with the shrub cover (Table 2).

Table 2: Correlations between tree cover, shrub cover and the number of Picea saplings in Marchairuz and La Sagne sites (n = 396). The p-values of the Spearman's rank correlation coefficient (rs) was corrected for spatial autocorrelation by Dutilleul's procedure (: P < 0.05; **: P < 0.01; ***: P < 0.001; n.s.: not significant). df is the corrected real-valued degrees of freedom accounting for spatial autocorrelation (17 distance classes).*

	Marchairuz site		**La Sagne site**	
	df	*rs*	*df*	*rs*
Shrub cover vs. *Picea* saplings	-	-	316.3	**0.261** ***
Tree cover vs. *Picea* saplings	138.2	**0.209** *	360.7	*0.029 n.s.*
Shrub cover vs. Tree cover	-	-	282.0	*-0.061 n.s.*

The multiple linear regression on tree cover by PCNM spatial structures appears to be significant for both sites, the variable procedure retaining in both cases PCNMs of large, medium and fine scale after accounting for possible gradient effects along X- and Y-axes (Table 3). Mapping part of these PCNMs illustrates these structures linearly combined to describe significantly the observed tree pattern (Figure 4).

Table 3: Selected PCNM spatial descriptors after the stepwise selection procedure in the multiple linear regression on tree cover in both sites (P < 0.001).

	Large scale PCNMs	**Medium scale PCNMs**	**Fine scale PCNMs**
Marchairuz site	1, 2, 11, 12	67, 79, 93	123
La Sagne site	1, 7	29, 40, 66	-

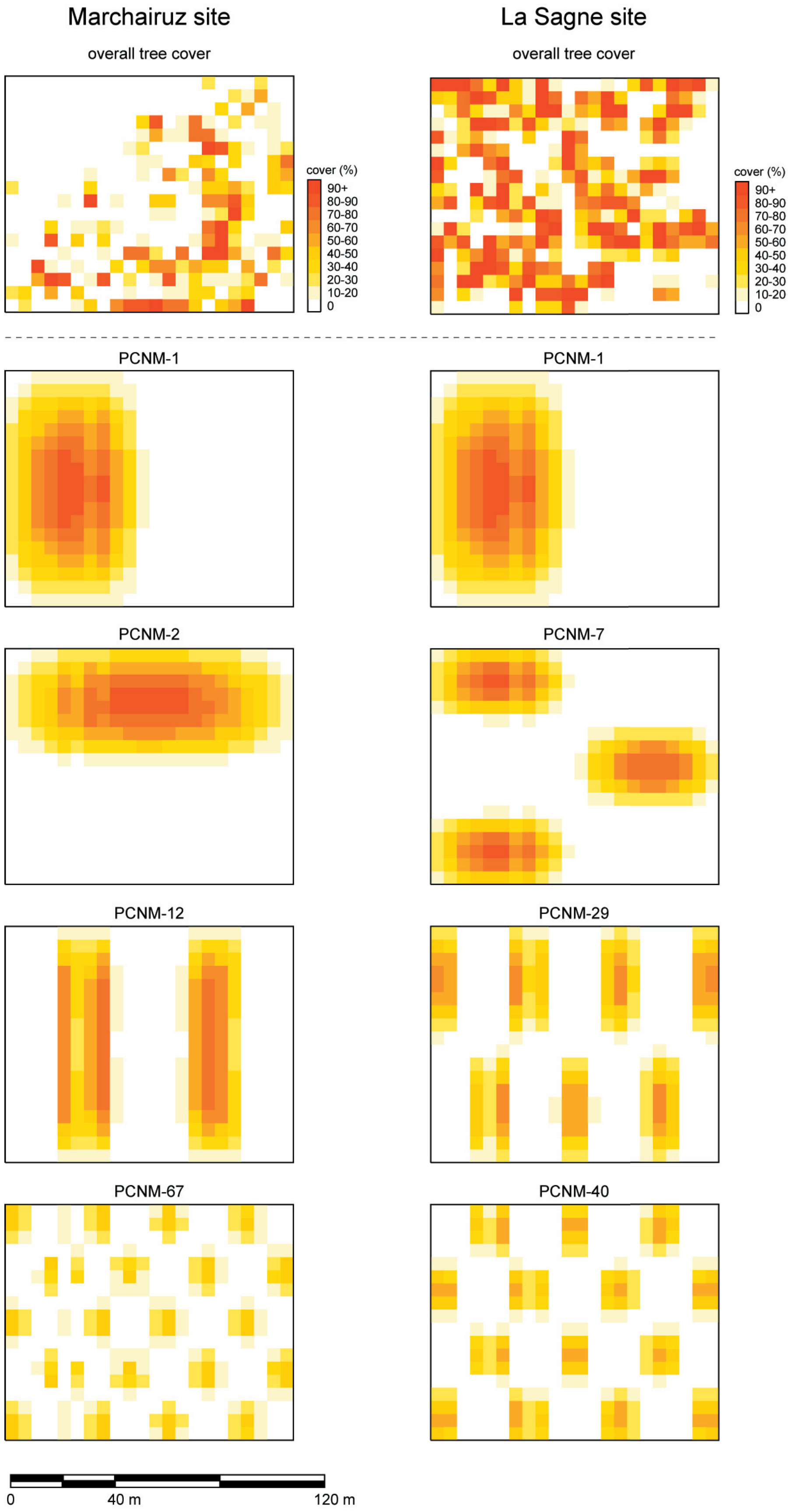

Figure 4: Examples of spatial structures generated with principal coordinates of neighbour matrices (PCNM) used as explanatory variables to describe the spatial structure of tree cover in a multiple linear regression (stepwise model selection, $P < 0.001$) for both sites.

Finally, the linear height-DBH model built on log-transformed DBH data appeared to highly significant (Table 4). Except a few outliers, the residuals after fitting display no clear structure and the Q-Q plot a rather linear structure on the X-Y diagonal (Figure 5). This let us conclude that for the size range of the trees we considered, the linear model fits well our allometry data.

*Table 4: Linear model of the log-transformed tree height on log-transformed DBH values, for both sites together. The significance of the model components tested using an analysis of variance (ANOVA). Model equation: ln(height) = 0.701*ln(DBH) + 0.306.*

Parameter	*df*	Sum of Squares	F-value	Pr(>F)
ln(DBH)	1	299.3	4493	2.2e-16
residuals	536	35.7		

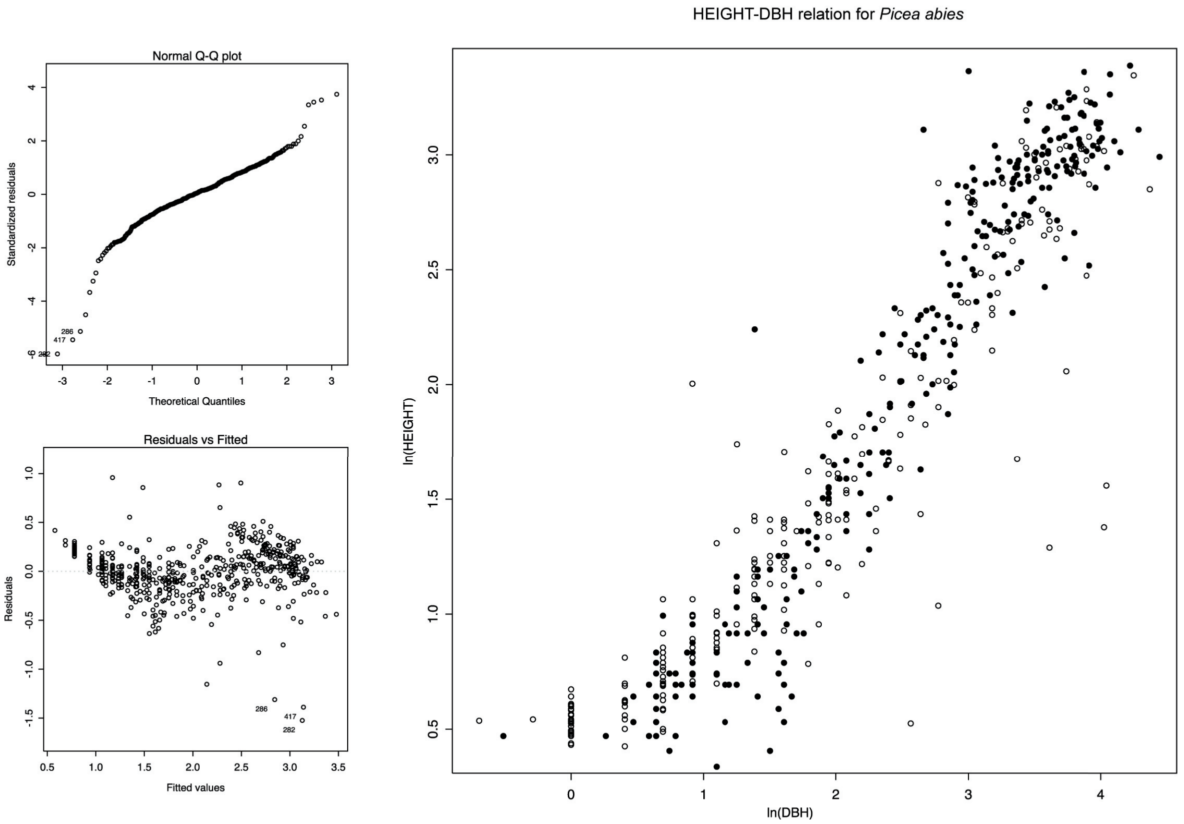

Figure 5: Relation between height and DBH of Picea abies trees on log-transformed data of both sites together (on the right) and structure of the residuals of the linear model of tree height built on site and log-transformed DBH variables (on the left). Black points: La Sagne site; white points: Marchairuz site.

Discussion

The height and DBH population structure of *Picea abies* showed in our case a partial gap between adult trees of the canopy and small sized trees, the medium-size trees being less abundant than expected in an balanced population (Gallandat et al. 1995), especially in La Sagne site. Such a discontinuity in the population size (and age) structure may reveal the lack of a stable equilibrium in the forest sub-system of wood pastures, due to present and past forestry and agricultural practices. It may highlight as well a possible management practice focussed on the systematic removal of trees of a certain stage within the shrub layer for example. The abundance of saplings and small trees let us expect possible consequences for such a man-made landscape in the future, the important tree recruitment indicating the potential evolution toward forested areas, if nothing is modified in the current management practices. This appeared to be more pronounced in the site of lower altitude and with free-ranging pasturing practices (La Sagne), these factors accelerating possibly the natural dynamics of the vegetation.

Furthermore in La Sagne site, the differences in tree species composition between trees over 1.5 meters (81.1 % among them are evergreen species) and saplings below 1.5 meters (64.7 % evergreen species) reveal at least partly the species specific impact cattle may have on tree recruitment. In a recent experimental field study however, Vandenberghe et al. (2007) observed surprisingly a lower survival rate for coniferous saplings of 10 to 15 cm height compared to deciduous saplings under both low and high grazing intensities, evergreen saplings loosing a larger proportion of biomass than deciduous trees. This difference in the tolerance to loss of biomass among tree species would mean that deciduous saplings have a priori more chances to survive in a height of 10 to 15 cm, overtopping more easily the surrounding herbaceous layer compared to *Picea abies* being more sensitive to browsing and competition from neighbours. But once above this height, the resistance strategies against cattle may then change in favour of evergreen species whose compensatory growth form advantages much more (see Chapter 5), which could explain the higher proportion of coniferous trees above 1.5 meters, despite their lower resistance within the herbaceous layer (Vandengerghe et al. 2007).

At La Sagne site, the spatial association between shrub cover and the amount of *Picea* saplings appeared to be positive and highly significant. This confirms our first hypothesis of enhanced tree recruitment with shrubs under grazed conditions. Our spatial analysis further revealed that the occurrence of *Picea* saplings was related to tree cover differently between the two study sites. In the Marchairuz site where no shrub occurred except small trees, *Picea* saplings were positively correlated to overtopping tree cover composed most exclusively by *Picea* trees, whereas in La Sagne site, this positive correlation did not occur any more with tree cover but with shrub cover.

This result could reveal the possible limiting effect of *Picea* seed dispersal in the Marchairuz site, but the long dispersal distance of these small winged seeds dispersed by the wind let us think about another explanation. As shown in previous studies, refuge structures such as shrubs or tree stumps provide safe sites for tree recruitment against cattle browsing (Smit et al. 2005, Smit et al. in press). This let us interpret our results as following: in the La Sagne case, shrubs play their protective role against browsing, either because of their mechanical protection by spines, their content in high levels of difficult-to-digest lignin or in secondary metabolites (Baraza et al. 2006, Gordon 2003), despite their possible competitive effect on tree saplings (Dolezal et al. 2004). On the other hand, in the Marchairuz site where the shrub layer was only occupied by small trees, trees often grow with branches close to the ground level even for tall adult trees, which can be considered as an indicator for a low browsing intensity. These low branches, occasionally responsible for vegetative reproduction through air layering (Laberge et al. 2001) can offer an alternative refuge site for tree recruitment, sheltering saplings against the trampling and browsing impact of cattle, despite growth suppression by dominant neighbours affecting light and soil conditions (Dolezal et al. 2006).

This let us conclude that the overtopping tree cover plays, in absence of other strong facilitation structure, the same protective role as shrubs do when present, being a nurse structure for tree recruitment in wooded pastures and confirming in this sense our second hypothesis. This result is consistent as well with Wilson and Agnew's one-sided positive feedback switch on tree regeneration (Wilson & Agnew 1992), and contrarily to Hewitt & Kellman (2002), we consider the effect of cattle pressure highly predominant against a possible seed trap effect of conifer trees in fragmented landscapes.

On the landscape management level, this result implies differentiated agricultural and forestry practices between such two sites aiming simultaneously for the conservation of traditional landscapes and a sustainable land use. In the case of a shrub-dominated wood pasture, the control made on cover and spatial structure of shrub communities is crucial in order to adjust the abundance and species composition of the coming tree cohort to the management goals. On the other hand, in the case of a wood pasture without shrubs, the control on the density and spatial structure of adult trees will be necessary to determine the optimal recruitment abundance and pattern for a long-term landscape management. Furthermore, the pruning of low branches, usually practiced in order to improve the wood quality in productive forests, would offer a suitable tool to reduce an abundant recruitment of *Picea* saplings. Cutting low branches would allow more favourable light conditions at the ground level, increasing the competition strength of the herbaceous layer towards

Picea saplings, allowing also cattle to affect regeneration by browsing and trampling. An increase of the cattle density would also reduce the density of low branches by a higher browsing pressure and the use of the understorey as shelter.

The analysis of the spatial structure of tree cover in both sites showed that the present tree cover could be described as a linear combination of spatial patterns at large, medium and fine scales, after accounting for possible gradient effects along X- and Y-axes. Each of these pattern, mathematically generated as PCNMs and contributing to the explanation of the variation in the observed tree cover above 1.5 meter high, resulted of numerous organisational processes occurring at comparable scales in the wood pasture system. Among such ecological processes generating patterns, previous studies provide us clues to interpret our results. The limitation by seed dispersal (Rammig et al. 2006), as well as cattle behaviour (Kohler et al. 2006) and topography (Dufour et al. 2006) contribute to the large scale component of the observed tree pattern. In addition, the intermediate scale component result at least partly of combined effects of the cattle behaviour (Kohler et al. 2006), intrinsic dynamic of shrub communities (see Chapter 6), edaphic conditions (Havlicek & Gobat 1998) and management practices applied at this scale, such as selective tree harvesting or shrub removal (Gillet 1996). Finally, the cattle selective grazing behaviour (Teague et al. 2004) and competition *vs*. facilitation processes (cf. previous chapters, and Smit et al. 2005) among the herbaceous and shrub layers contribute in generating the fine scale component of tree cover.

Concluding, the combination of spatial patterns at large, intermediate and small scale reveal the complexity of multifunctional landscapes such as wood pastures, where numerous interacting processes belonging to specific spatio-temporal scales. In such a context, hierarchical approaches become relevant tools for further investigations (Bragg et al. 2004, Noda 2004), setting the framework for further research, conservation and management purposes. Integrative modelling perspectives raise, requiring data on time scales related to tree recruitment and growth. Among those further investigations, detailed tree growth analysis are needed, with the help of aerial photographs and dendroecological investigations. Our basic allometric model can therefore be useful in order to save time in collecting tree height and DBH data, and to further calibrate growth models of individual trees. Growth response to browsing exposure and competition with neighbour trees are the next key issues for a better understanding of patterns and underlying processes towards a synthesis of the role of trees as key species in wood pastures.

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CHAPTER 5

Annual growth dynamic of *Picea abies* under browsing pressure: an original method and major outcome

Introduction

Tree growth is a major outcome in understanding patterns and dynamics of forested systems. Understanding relations between tree morphology and external constrains such as site characteristics (Kunstler et al. 2005), neighbourhood (Stancioiu & O'Hara 2006), climatic conditions (Cunningham et al. 2006), biotic constrains (Husheer et al. 2006) and human activities (Hessl & Graumlich 2002) are of great interest for the resource management and landscape planning. Numerous models were elaborated in order to provide development scenarios over time depending on tree density (Andreassen & Tomter 2003), climate (Nuutinen et al. 2006), external disturbances (Rammig et al. 2006) or land use frequency and intensity (Bergez et al. 1999), with few integrative attempts (e.g., Bragg et al. 2004).

Among the numerous factors affecting tree growth, biomass removal by herbivores is an important one (Janzen 1970, Dyer et al. 1993). It has been investigated in a wide range of ecosystems, from temperate forests (Ammer 1996) to savannahs (Rooke et al. 2004b). Wild and domesticated herbivores have been shown to have major effects on woody species recruitment, plant architecture (Rooke et al. 2004a), height growth (Vila et al. 2003), leaf characteristics (Ruusila et al. 2005) and species selection (McIntyre et al. 2003). The degree of growth loss, stem deformation and likelihood of death from browsing increase with the severity of damage (Gill 1992). On the other hand, compensatory growth was often observed on trees as response to browsing (Belsky et al. 1993, Hjalten et al. 1993, Rooke et al. 2004a). Such a growth reaction was considered by Edenius et al. (1993) as a plastic trait in slow growing coniferous woody plants, not necessarily a specific adaptation to herbivory. Consequently, tree allometry gets modified and standard growth equations established for trees in undisturbed growth conditions have to integrate the impact of herbivores in order to be efficient.

Tree allometry has been studied over several decades (Zianis and Radoglou 2006, Fehrmann & Kleinn 2006, Muukkonen & Makipaa 2006). The development of the trunk and the shape of the crown are strongly dependant (Cancino et al. 1999, Choi et al. 2001). Tree height, diameter at breast height (DBH) and branch diameter are strongly correlated and several models have been proposed for a wide range of areas and species in the world (e.g., Clark & Clark 1999, Fehrmann & Kleinn 2006).

Norway spruce (*Picea abies* L. Karst) is the largely dominant tree species in mountain forests of Central Europe, and has widely been used as wood resource over centuries. Many studies were carried out on the regeneration (e.g., Hofgaard 1993, Brang 1998, Pagès et al. 2003), growth (e.g., Sterba et al. 2001) and physiology (e.g., Zweifel & Hasler 2001). The dynamics of crown shape of Norway spruce was described since a while (van Laar 1976, Gruber 1990, Pretzsch & Schutze 2005), in relation with aboveground and belowground biomass (Drexhage & Gruber 1999, Puhe 2003, Petersson and Stahl 2006), as well as for branchiness (Colin & Houllier 1992). Furthermore, the branch length increment was modelled by Deleuze et al. (1996) on few young trees, and knot properties predicted from generic tree descriptors for the purpose of timber utilization and wood quality (Moberg 2006). Relation to climate and shading were investigated recently as well (Weisberg et al. 2005, Cunningham et al. 2006).

In the wooded pastures of the Swiss Jura mountains, *Picea abies* is the most dominant tree species of the forest sub-system, determining underlying patterns and processes involving in particular herbaceous vegetation and cattle grazing seasonally in the system (Gillet et al. 2002, Kohler et al. 2006). Many studies were achieved on *Picea abies* in forested stands, but the growth of isolated trees growing under the influence of herbivores has received little attention yet.

The analysis of damages caused by herbivores on trees showed a linear relation between the stocking density and the proportion of browsed or damaged trees (Mayer et al. 2006). Furthermore, a preferential browsing behaviour of cattle and a subsequent differentiated sapling survival among common wooded pasture tree species was observed in recent experimental studies (Vandenberghe et al. 2007). *Picea abies* was appearing as the least competition tolerant species as shown previously by others (Pagès et al. 2003, Heuze et al. 2005). On *Picea abies* saplings, Vandenberghe et al. (2007) observed no compensation events, possibly explained by the delayed growth response highlighted by others (e.g., Haukioja & Koricheva 2000) and by the more severe consequences summer browsing have on tree recruitment (Canham et al. 1994, Relva & Sancholuz 2000, Harmer 2001). Nevertheless, long-term data and detailed tree growth analysis form field observations are mainly missing for *Picea*-dominated wooded pastures yet.

In this paper, we aimed to present an original none-destructive method to investigate past apical growth of *Picea abies* trees, as well as some results and perspectives it offers in the investigation of the growth on browsed *Picea* trees in wood-pastures. The following hypotheses will be explored: (i) both apical and lateral growth are reduced for small *Picea* trees under grazing regime in a wood-pasture compared to growth in an open but none-grazed situation; (ii) growth reduction occurs until the tree reaches a certain threshold in its height; (iii) above this height, the growth rate reaches or even overpasses the one of non-browsed trees.

Material and methods

Study site

The study was carried out in a wood-pasture of the Swiss Jura Mountains, in the Parc jurassien vaudois (Sèche des Amburnex, Le Chenit VD, altitude 1340 m a.s.l., 6°13'E, 46°33'N). The research site was chosen to offer a pastured and an abandoned stand close to each other, both in a similar geomorphological and vegetation context. Both stands of at least one-hectare are dominated exclusively by Norway spruce (*Picea abies*) with a tree cover below 50% and a wide range of tree sizes. The calcareous topography is SE-orientated with gentle slope in both stands, generally with shallow soils covered by typical mountainous grassland communities. The pastured stand has continuously been used for at least a century for summer cattle grazing, whereas the abandoned stand belonging to the same management unit was not pastured any more for the last 20 years (farmer; comm. pers.).

Data collection

The field work was carried out in October and November 2003, at the end of the vegetation and grazing season. In each two stand, 12 *Picea abies* trees of 1 to 4 meters height were randomly selected from an initial inventory of all *Picea* trees of this size range in each stand, following a stratified selection strategy. Eight trees where selected for the height range of 2 to 4 meters, whereas four additional trees were taken between 1 and 2 meters high. These height ranges were chosen suspecting a possible change of the growth rate around the cattle height. A minimal distance of 4 meters to a higher neighbour tree was set to minimize the possible influence of the competition at the canopy level with higher or neighbouring trees.

On the 24 sampled trees, a branch of each whorl of branches was randomly selected, cut as close as possible to the stem and collected. On each branch, the transversal *Lt* length along the orientation of its insertion in the stem was measured (woody part only), as well as the maximal *Lmax* length stretching the branch flat (Figure 1). This second measure was made in order to assess the possible effect of browsing on the branch shape, browsed branches often displaying a higher lateral expansion relative to the length along the main growth axis (Figure 1). The height of insertion *Hi* from the ground level was further measured. Whether the overtopping ramification was along the main growth axis or not was recorded with a binary variable,

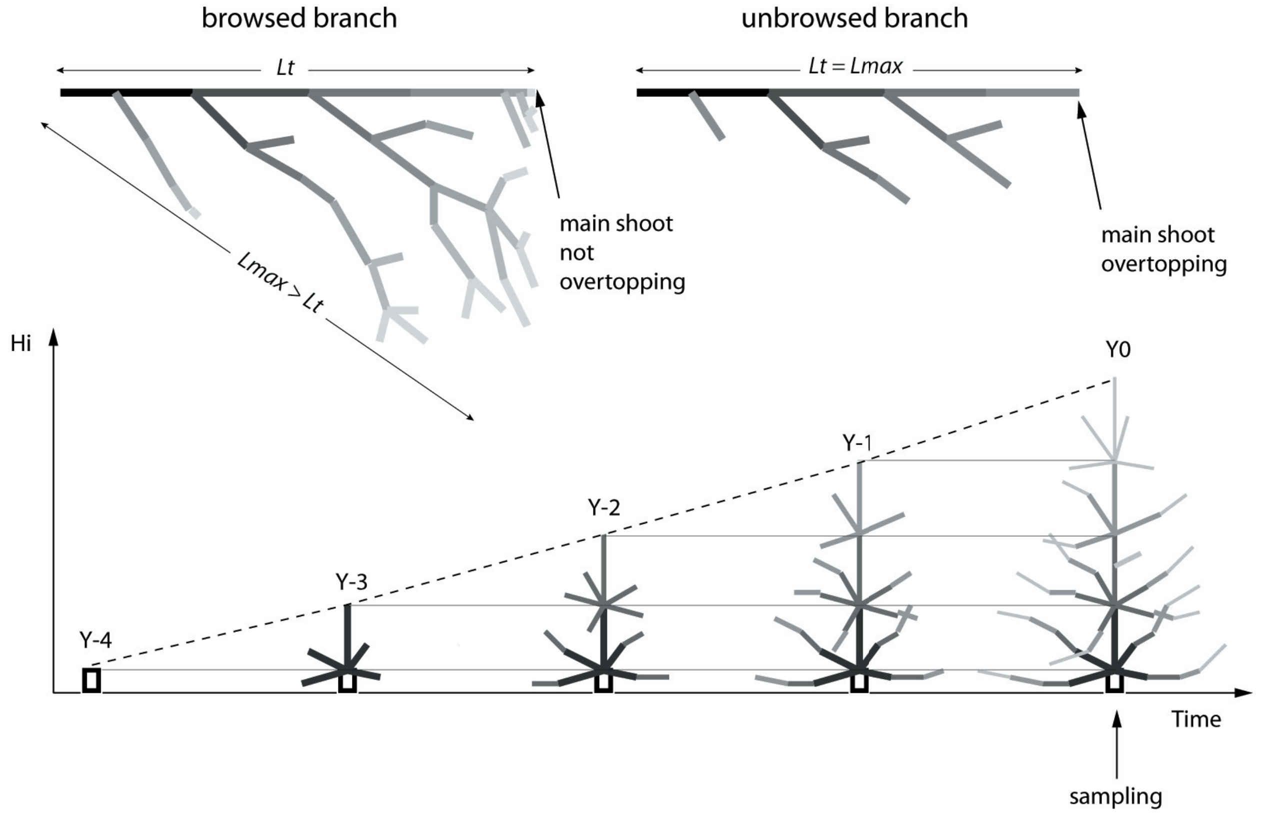

Figure 1: Schematic height and lateral growth of Picea tree derived from the branch structure and aging. Each year Yi under favourable growth conditions, a new whorl of branches appears at the level Hi of the apical bud. Meanwhile, the apical bud raises along the stem orientation up to next years' whorl reaching the maximal height Hi+1. Furthermore, new ramifications or extensions may appear at the edge of existing branches, sometimes along an older segment. Under browsed conditions, compensatory growth of lateral ramifications was observed, the shoot along the main growth axis not overtopping the overall shape of the branch, and maximal branch length Lmax being different from the length Lt measured along the main growth axis.

an overtopping ramification not along the main growth axis interpreted as a further consequence of browsing (Figure 1). The age *Yi* of each branch was then determined by counting the number of tree rings at the cutting edge under a stereo binocular.

In order to validated the tree age estimation from the ring count at the branch cutting edges, the stem was cored with an incremental borer in order to reach the stem pith and as close as possible to the ground, recording additionally the coring height. The number of tree rings was then counted as well under a stereo binocular.

At the edge of each branch, the last years' growth (i.e. annual growth 2003) was cut and dried separately from the remaining part of the branch. The dry leaf and wood biomass was then sorted and weighted separately for the entire branch and the last years' growth.

Data analysis

Assuming that the branch started its growth in the highest whorl corresponding to last years' top height, the curve $Hi = f(Yi)$ representing the evolution of the last whorls' height over time was then interpreted as a height growth curve of the sampled tree (Figure 1). For each tree, the height growth curve was plotted, taking as origin along the time axis the moment of sampling, and considering tree growth retrospectively from the present point. A scatter plot smoothing curve was added (Cleveland, 1979). Possible synchronisms in the growth curves may by the mean reveal possible events such as particular climatic or management conditions affecting all trees simultaneously. From the 'branch' point of view, the overall tree height was considered as the height for branches with $Yi = 0$.

For each branch collected at the height *Hi*, a Annual height increment *dH/dt* of the tree stem at height *Hi* was calculated as following:

$$dH/dt = (Hi+1 - Hi)/\ (Yi - Yi+1)$$

The branch mean growth rate *dL/dt* was estimated for each branch from its length and age as following:

$$dL/dt = Lt\ /\ Yi$$

Furthermore, a browsing index *BI* was derived as a ratio between both branch lengths:

$$BI = Lt\ /\ Lmax$$

In case of an ‘unbrowsed’ branch, $BI = 1$, and for a ‘browsed branch $BI < 1$ (Figure 1). For the last years’ branch fraction, a leaf/wood ratio was calculated, representing the proportion of biomass allocated to the production of leaves compared to wood production.

In order to reveal possible thresholds of branch allometry according to their insertion height, a clustering method constrained on insertion height was applied out on the subset of browsed branches, defining consistent branch height classes. Therefore, the minimum variance clustering method was used to discriminate branches according to their dissimilarity in corresponding annual height increment *dH/dt* and insertion height *Hi*. Dissimilarity was estimated by Euclidean distance between square-root transformed data. Within the resulting height classes, the differences between browsed and unbrowsed branches were tested on annual height increment, branch mean growth rate and leaf/wood ratio using unpaired Wilcoxon signed rank tests.

Constrained minimum variance clustering was computed on MVSP 3.13 (Kovach Computing Services 2006) and Wilcoxon signed rank tests with the software R 2.4.0 (R Development Core Team 2006).

Results

On *Picea* trees growing under browsing pressure, between 9 and 20 branches per tree were sampled. At a coring height varying between 11 and 28 cm, the age got from stem ring count ranges between 17 and 37 years for an overall height of 1.1 to 3.6 meters (Table 1). On the non-browsed *Picea* trees, between 12 and 19 branches per tree were sampled. At a coring height varying between 15 and 34 cm, the age got from stem ring count ranges between 18 and 34 years for an overall height of 1.5 to 4 meters (Table 1).

Table 1: Overall height, number of sampled branches and tree age estimated by tree ring counting at coring height for the 12 sampled Picea abies trees in each pastured (browsed trees) and abandoned pasture (unbrowsed trees).

Sampled tree	Overall height (cm)	Nb. sampled branches	Age at stem coring
	BROWSED TREES		
AM01	270	19	22 y. at 22 cm
AM02	170	13	17 y. at 19 cm
AM03	237	17	27 y. at 24 cm
AM04	252	15	28 y. at 25 cm
AM05	356	20	25 y. at 17 cm
AM06	113	12	24 y. at 20 cm
AM07	216	13	30 y. at 25 cm
AM08	137	9	23 y. at 21 cm
AM09	294	16	37 y. at 11 cm
AM10	178	13	29 y. at 28 cm
AM11	286	14	22 y. at 23 cm
AM12	339	18	30 y. at 25 cm
	UNBROWSED TREES		
SA01	264	19	28 y. at 25 cm
SA02	298	15	19 y. at 26 cm
SA03	194	14	21 y. at 23 cm
SA04	398	18	20 y. at 34 cm
SA05	264	17	22 y. at 25 cm
SA06	273	18	28 y. at 25 cm
SA07	344	14	24 y. at 24 cm
SA08	201	15	33 y. at 19 cm
SA09	195	14	23 y. at 18 cm
SA10	249	14	34 y. at 24 cm
SA11	219	13	25 y. at 22 cm
SA12	151	12	18 y. at 15 cm

Tree height growth curves of browsed and unbrowsed trees show similar overall shapes (Figures 2 and 3). Indeed, an inflexion of the curve is observed for browsed trees between 1.0 and 1.5 meters, appearing more or less significantly depending on individual trees, compared to unbrowsed trees displaying a more regular growth shape. Small browsed trees (height between 1 and 2 meters) display more irregular shapes, revealing the growth of trees not necessarily escaped from cattle influence in their height growth (especially AM06; Figure 3).

Displaying branch growth rate as a function of height, individually for each browsed and unbrowsed tree, illustrate the branch growth general shape along the tree (Figure 4). Below 1.0 to 1.5 meters, branches of browsed *Picea* trees show reduced growth which seems to be released once above (Figure 4).

The constrained clustering of browsed branches defined six height ranges along the stem: (i) 0 to 0.2 m; (ii) 0.2 to 0.6 m; (iii) 0.6 to 1.4 m; (iv) 1.4 to 1.65 m; (v) 1.65 to 2.3 m; (vi) 2.3 to 3.5 m.

Branches inserted below 0.2 meters show a higher branch mean growth rate in browsed conditions (unpaired Wilcoxon signed rank test: $W = 30.5$, $P = 0.018$), with a lower leaf/wood ratio (unpaired Wilcoxon signed rank test: $W = 140$, $P < 0.001$). In both conditions, branches are mostly without an overtopping edge who corresponds to the main growth axis.

Branches inserted between 0.2 and 0.6 meters don’t differ in branch growth rate between browsed and unbrowsed conditions. the leaf/wood ratio remains lower under browsing (unpaired Wilcoxon signed rank test: $W = 1462$, $P < 0.001$). Below 0.6 meters, the tree annual height increment does not differ between browsed and unbrowsed conditions.

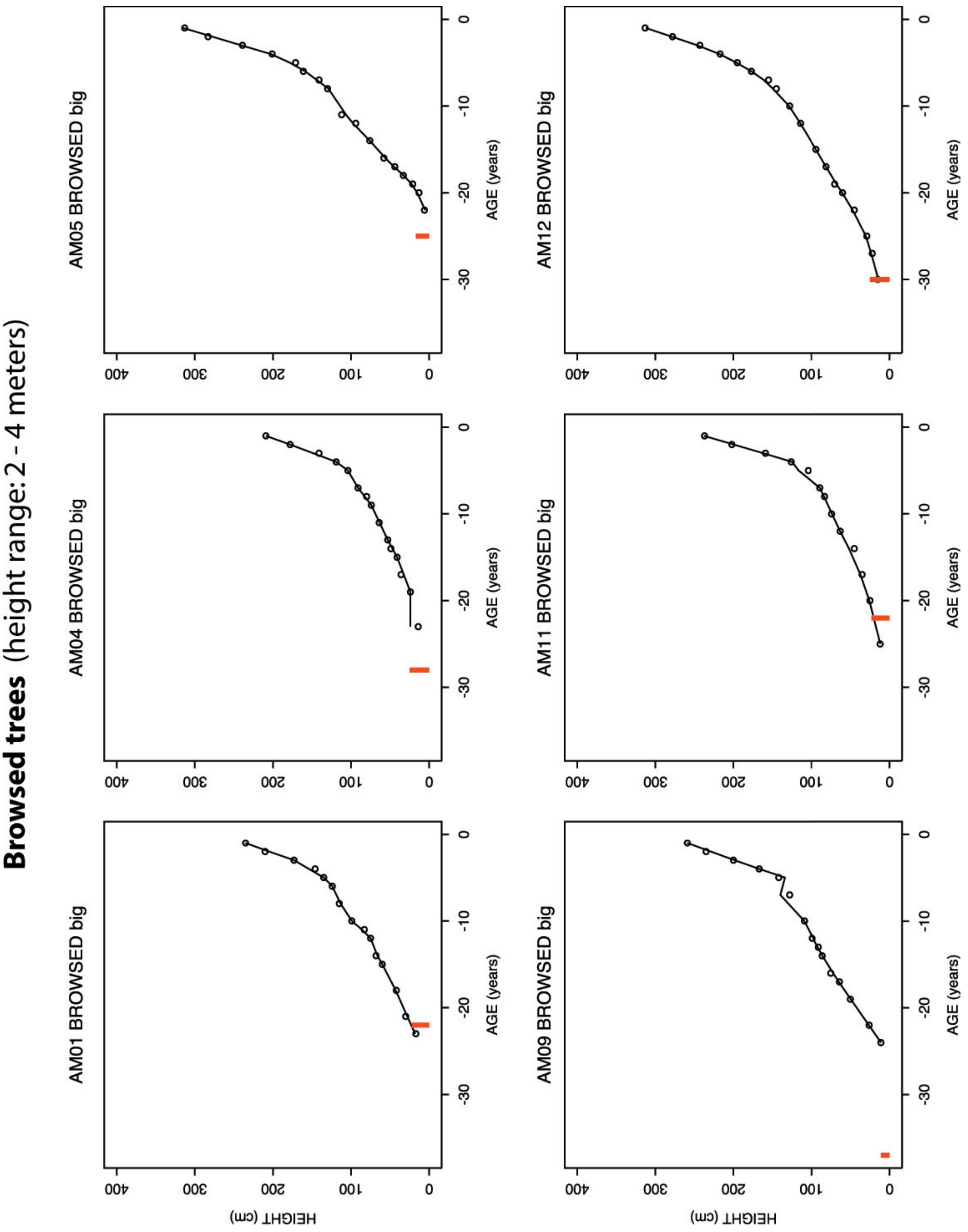

Figure 2a: Height growth curves of Picea trees of 2 to 4 meters under browsed conditions, rebuilt from the aging of branches collected at each whorl and a plot smoothing curve. For each tree, the age measure obtained from stem coring and ring counting is indicated with the bold mark at the corresponding coring height.

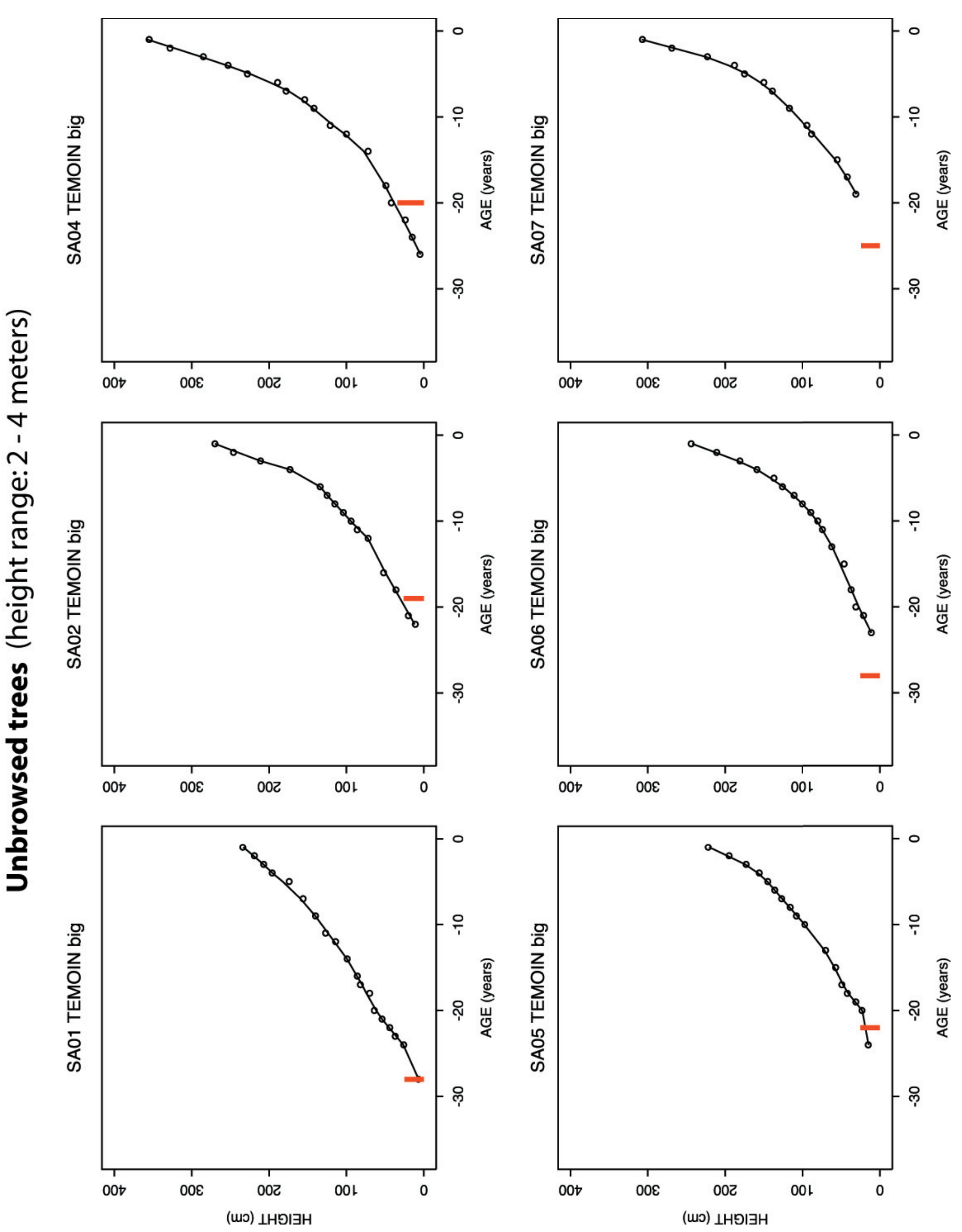

Figure 2b: Height growth curves of Picea trees of 2 to 4 meters under non-browsed conditions, rebuilt from the aging of branches collected at each whorl and a plot smoothing curve. For each tree, the age measure obtained from stem coring and ring counting is indicated with the bold mark at the corresponding coring height.

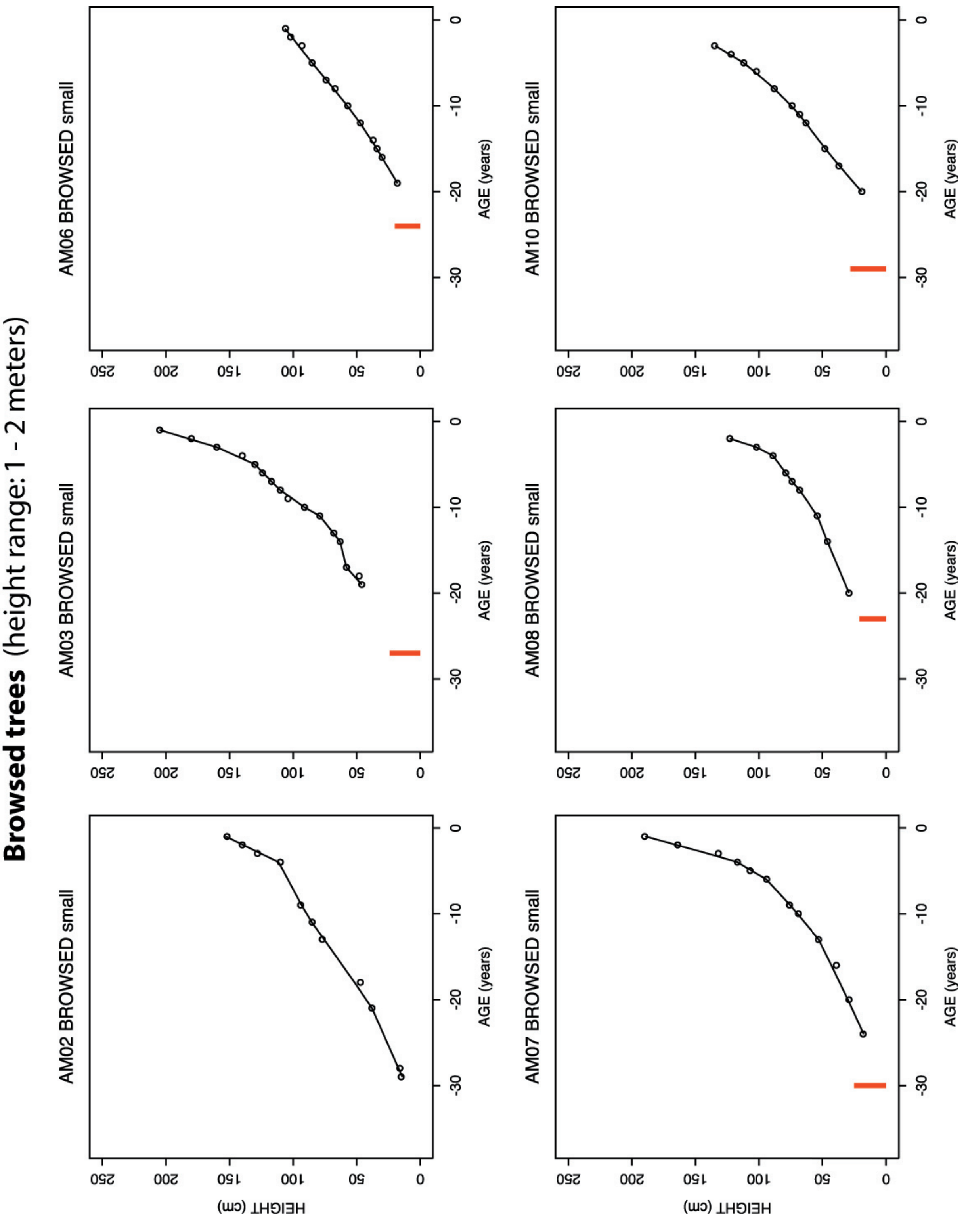

Figure 3a: Height growth curves of Picea trees of 1 to 2 meters under browsed conditions, rebuilt from the aging of branches collected at each whorl and a plot smoothing curve. For each tree, the age measure obtained from stem coring and ring counting is indicated with the bold mark at the corresponding coring height.

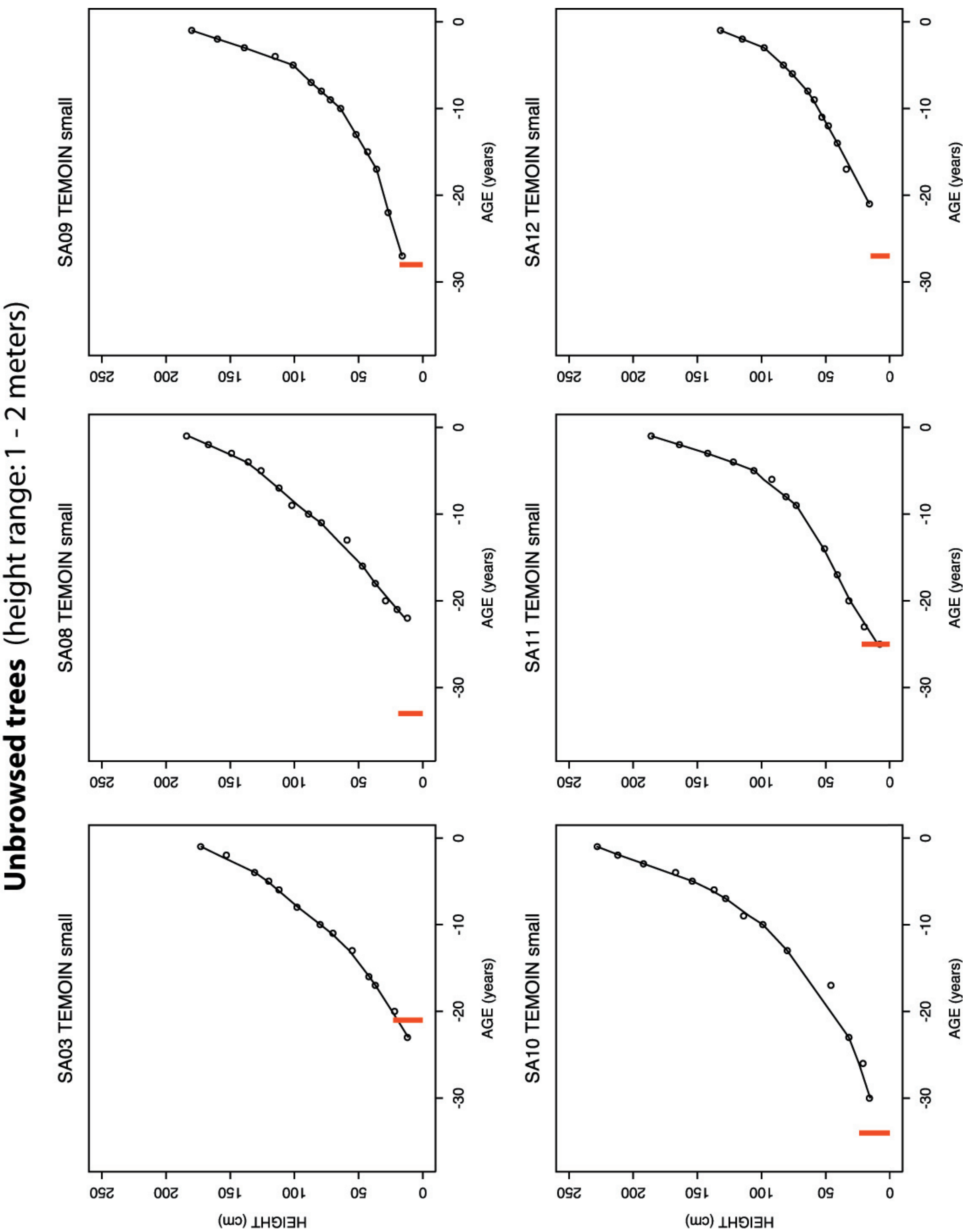

Figure 3b: Height growth curves of Picea trees of 1 to 2 meters under non-browsed conditions, rebuilt from the aging of branches collected at each whorl and a plot smoothing curve. For each tree, the age measure obtained from stem coring and ring counting is indicated with the bold mark at the corresponding coring height.

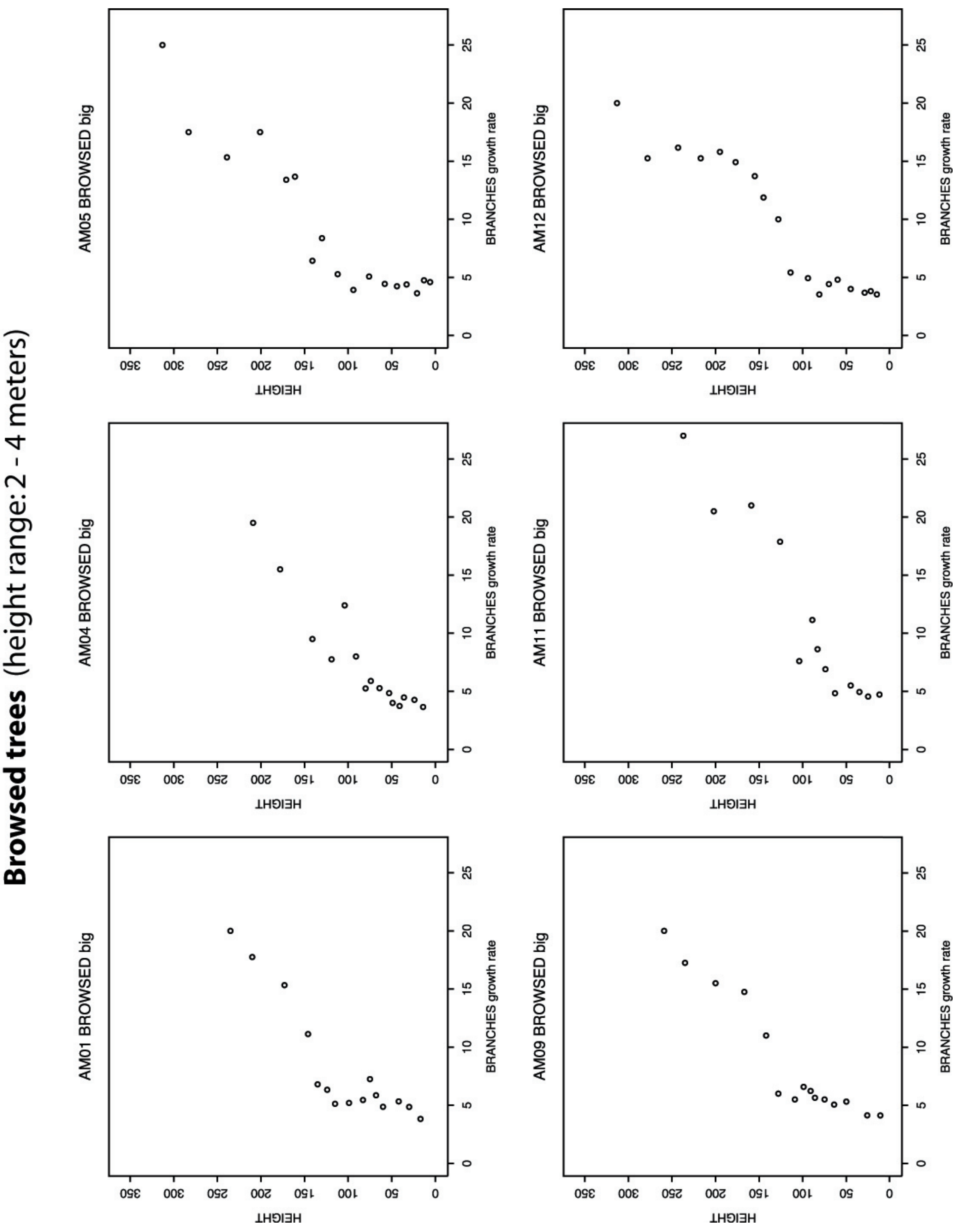

*Figure 4a: Branch mean annual growth rate dL/dt (in cm*year^{-1}) at their insertion height (in cm) on the stem, for each sampled tree under browsed conditions.*

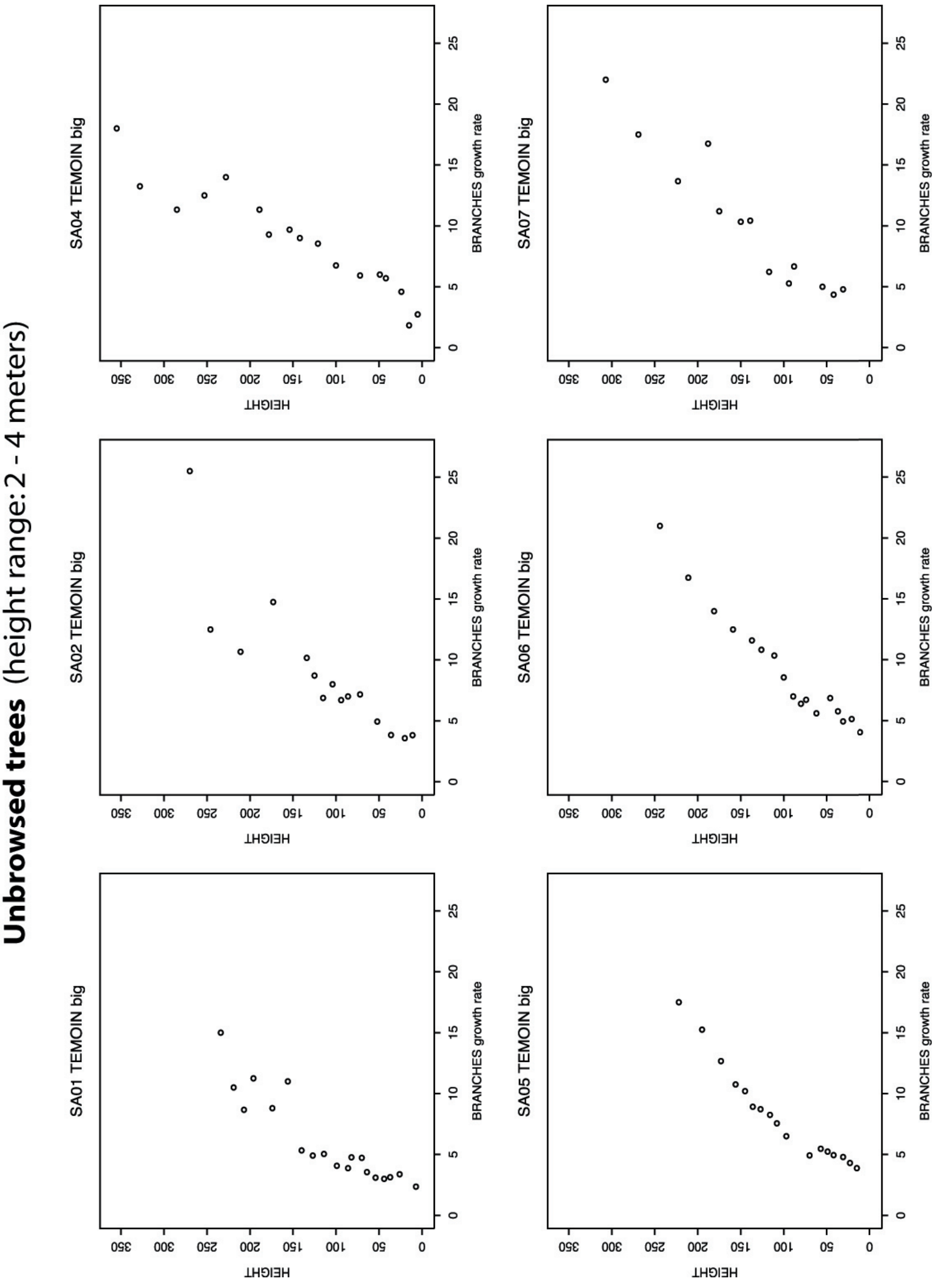

*Figure 4b: Branch mean annual growth rate dL/dt (in cm*year^{-1}) at their insertion height (in cm) on the stem, for each sampled tree under non-browsed conditions.*

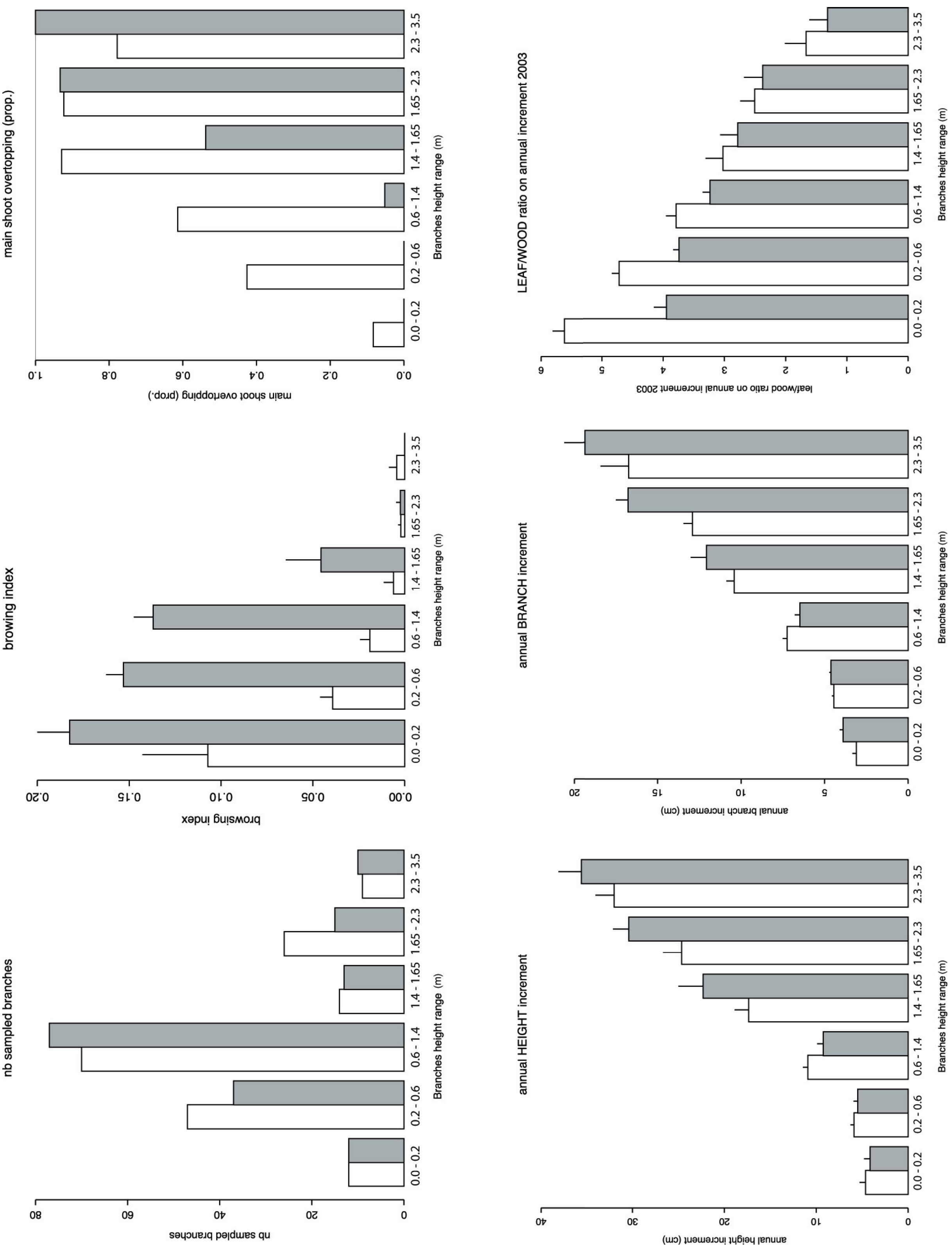

Figure 5: *Branch number, browsing index BI (mean + 1SD), proportion of overtopping main shoots, Branch annual growth rate (mean + 1SD), corresponding tree Annual height increment (mean + 1SD) and leaf/wood dry biomass ratio on last years' branch increment (mean + 1SD) of browsed and unbrowsed Picea branches. Height ranges correspond to growth limits defined by the constrained height clustering established for browsed trees. Grey: browsed trees; white: unbrowsed trees.*

Branches inserted between 0.6 and 1.4 meters display strong differences between browsed and unbrowsed conditions: under browsing pressure, branch mean growth rate is lower (unpaired Wilcoxon signed rank test: W = 3442.5, $P < 0.001$), as well as the leaf/wood ratio (unpaired Wilcoxon signed rank test: W = 3504, $P = 0.0017$). Meanwhile, tree height growth is reduced (unpaired Wilcoxon signed rank test: W = 3544.5, $P < 0.001$). Overtopping main shoots occur on 61% of unbrowsed branches, whereas only few of them are overtopping under browsing (5.2%; Figure 5), displaying the typical 'browsed' shape (Figure 1). The comparison of the browsing index shows the same tendency.

Between 1.4 and 1.65 meters height, no significant differences are observed anymore between browsed and unbrowsed trees. Close to 1 for unbrowsed trees, the main shoot overtopping proportion raises up to 0.54 under browsing conditions (Figure 5).

Above 1.65 and up to 2.3 meters, branches characteristics reveal other differences. Branch growth is higher in browsed conditions compared to the absence of browsing (unpaired Wilcoxon signed rank test: W = 60.5, $P < 0.001$). Furthermore, the annual height increment is slightly higher as well under browsing (unpaired Wilcoxon signed rank test: W = 122, $P = 0.049$). The proportion of main shoot overtopping are comparable between both growth conditions (Figure 5).

Once above 2.3 meters, no differences are observed anymore on *Picea* trees growing under browsing pressure. The annual height increment passes beyond 30 cm per year. and branches at this height show a vigorous growth rate between 16.7 and 19.4 cm per year (Figure 5).

Discussion

Discontinuities in the height growth pattern of browsed trees appear clearly, revealing consistent functional height levels, as detailed analysis on growth and biomass allocation show. During its life cycle, the *Picea* tree will have to overcome these height levels, implying a succession of external constraints and possibly induced adaptative responses for the tree. The branches inserted at a given height most probably started to growth at the time the small tree was at this height. Afterwards and while the tree is growing, those branches remain at this height, their growth being further affected by the ecological constraints affecting the tree at this height over ground level. This let us have the following interpretation of our observations:

At the first functional height level from the ground up to 0.2 meters, branches show surprisingly a higher branch mean growth rate under browsing pressure compared to unbrowsed conditions. We interpret this as a compensatory branch growth of browsed trees at low height, branches benefiting of better light conditions due to suppressed branches growing above and balancing the strong pressure occurring higher. In addition, such low and usually slow-growing branches may not be attractive for cattle, the major process constraining growth being at this height level mostly competition for light within or just above the herbaceous layer. This compensatory growth of low branches may also offer an efficient response by slowly ‘pushing’ cattle away from the apical bud, explaining the particular pyramidal shape sometimes observed in the field (obs. pers.).

The lower leaf/wood ratio observed on one year shoots of browsed branches correspond to a proportionally higher wood compared to needles proportion. Beside the common trend of a decreasing leaf/wood ratio with increasing tree height (Figure 5), this higher wood production relative to needles may be an adaptative growth response of browsed *Picea* branches below the upper browsing limit at 1.4 meters. The lower concentrations of nitrogen or high concentrations of fibre in woody branch parts may also reduce palatability, improving chemical and structural resistance against herbivores (Lundberg & Danell 1990, Augner 1995).

At a height ranging between 0.2 and 0.6 meters, branches seem to bear a low browsing pressure which does not affect tree height and branch growth rates. Free of competition with the surrounding vegetation, branches are mainly under the constraint of herbivores, and the *Picea* tree are clearly visible at this height and further above. The absence of compensatory growth on lower branches of browsed trees may possibly be due to a simultaneous biomass removal by browsing cattle at this height.

At the third functional height level ranging between 0.6 and 1.4 meters, the impact of browsing is found to be the highest: on browsed *Picea* trees, a lower branch mean growth rate reveal a regular and strong impact of browsing, reducing branch elongation and modifying its architecture with a lateral expansion, the main growth axis rarely overtopping the branch shape. This increases the density of the canopy and may offer a higher mechanical resistance to herbivores, confirming our first hypothesis of reduced growth under browsing pressure. Similar results were found by Vila et al. (2003) on another conifer species (*Tsuga heterophylla*) affected by deer browsing, short compact and ramified branches offering a higher resistance to herbivores. Meanwhile, the lower height growth rate reveals suppressed height growth when the tree was at that size. With a mean growth rate of 9.2 cm per year at this height, it will take in average eight to nine years for the tree to reach a height above heavy browsing pressure (i.e. one or two years more than the unbrowsed trees of our study). Compared to Bergquist et al. (2003), who found that three successive years of simulated browsing by branch clipping reduced height growth by the equivalent of about one year, our results show effects of a medium browsing pressure, corresponding to the extensive pasturing in our study site.

Above 1.4 meters, our results indicate that isolated *Picea* trees escaped mostly from browsing pressure. In this fourth functional height level up to 1.65 meters, constraints on branch and height growth are released and branches of browsed trees do not differ anymore from branches of unbrowsed trees, confirming our second hypothesis.

Above 1.65 and up to 2.3 meters high, tree height growth and branch growth both display a compensatory growth response in case of browsed trees, confirming as well our third hypothesis. Such an over-compensation (i.e. regrowth capacity) was already observed by others on browsed trees and shrub species (Hjalten et al. 1993, Skarpe & van der Wal 2002, Rooke et al. 2004a), after dry-season browsing in African savannas (Dutoit et al. 1990, Dangerfield & Modukanele 1996, Bergstrom et al. 2000) and on birches in boreal forests (Danell et al. 1997). Even if slow-growing, low-resource-adapted plant species such as *Picea abies* is expected to invest in chemical defences against herbivory (Bryant et al. 1983, Coley et al. 1985), *Picea abies* precisely seems to adopt at least partly its regrowth strategy to resist against herbivory (Vandermeijden et al. 1988, Herms & Mattson 1992). This overcompensation can also partly be interpreted as an indirect effect of the recovery of previously suppressed apical dominance of *Picea abies* growth.

Once above 2.3 meters, nothing distinguishes browsed and unbrowsed *Picea* trees anymore in their height and branch growth rates. At this height, trees can be considered as having completely escaped the influence of browsing by cattle.

As additional remark, the important differences between the age sometimes obtained from ring count on the stem and aging the lowest sampled branch reveal a long period of reduced growth under harsh conditions at a size below 20 cm (Figures 2 and 3), investigated partly by others in previous studies (e.g., Vandenberghe et al. 2007) and that we will not discuss in detail here.

Finally, our study proves that tree height and branch growth rates can reveal the impact of browsing by cattle both under direct pressure. It further shows that repeated and intense browsing on isolated *Picea abies* trees result in reduced height and lateral growths, in compact and heavily ramified branch shape below 1.4 meters high. Once above the height limit of 1.4 meters and after a compensatory growth during 2-3 years until the tree reaches the height of 2.3 meters, the tree escaped from browsing influence and its growth pattern cannot be distinguished anymore from unbrowsed trees.

In addition to reduced height and branch growths, as well as differentiated leaf/wood allocation under browsing pressure, *Picea abies* trees display few other growth particularities described in the literature and often observed in the field, improving their recruitment in grazed systems. Hence, *Picea abies* frequently become multi-trunked and/or develop multiple leaders under browsing (Ponge et al. 1994). Bergquist et al. (2003) further observed that *Picea abies* was particularly prompt to growth in stunted agglomerated clones. From air layering (called '*marcottage*' in french), an underground branch becomes an independent stem close to the main stem (Brennan & Mudge 1998, Laberge et al. 2001). Despite the high intraspecific competition, it offers the advantage of neighbouring branches to be protected against browsing. All these adaptative growth strategies certainly explain the high dominance of *Picea abies* in the montaneous silvopastoral ecosystems of Central Europe.

Concluding, our results provide useful information on the growth pattern of isolated *Picea* trees under the constraint of browsing by cattle, and will contribute in a better understanding of the temporal dynamic of the forest sub-system of wood pastures. Further detailed investigations should be carried out on stem growth analysis and on long term study under simulated browsing for a better functional understanding of underlying processes. Detailed growth investigations on small *Picea* trees competing within the herbaceous layer and supporting the mechanical damage of snow weight should be undertaken, as well as the possible influence of browsing on wood anatomy such as resin ducts (Nagy et al. 2000) or latewood density (Wimmer & Grabner 2000), which would allow a retrospective inference on past land use in silvopastoral systems.

CHAPTER 6

Tree replacement in wooded pastures: Tree stumps contribute to shrub and tree recruitment

Introduction

Natural and human disturbances are at the basis of the spatio-temporal dynamics of forested ecosystems (Sousa 1984, Kuuluvainen 1994, Nakashizuka 2001), including Norway spruce (*Picea abies* L. Karst) temperate forests (Cherubini et al. 1996, Holeksa & Cybulski 2001). Created by natural tree death and tree cutting, gap openings in the forest canopy often the initializes a new woody species succession, and gapfiller tree species are mostly different species than previously standing tree species (e.g., Lertzman 1992). In the context of tree regeneration, tree stumps have been shown to play an important role on recruitment (Chapter 1; Barker & Kirkpatrick 1994, Jonsson 1999, Narukawa & Yamamoto 2001, Nakagawa et al. 2003). Lertzman (1992) showed in particular that tree stumps were the only favourable circumstances for a direct recruitment of the tree species whose fall or cutting created the forest gap, replaced elsewhere by other tree species. But, the regeneration on those microsites is not necessarily sufficient to insure enough tree regeneration (Nakagawa et al. 2003).

In *Picea abies*-dominated boreal forests, decomposing wood from logs and stumps was shown to serve as nurse structures for the recruitment of *Picea* saplings (Hofgaard 1993a, Hornberg et al. 1997, Jonsson 1999), the continuous presence of decomposing wood allowing the maintenance of the tree population structure favourable for a long-term structural stability (Hofgaard 1993b). The elevated position (Hornberg et al. 1997) and the specific soil conditions due to the decomposition of below-ground biomass being favourable to diverse communities of ectomycorrhizal fungi (Dickie et al. 2002) were often assumed to contribute positively in the tree recruitment conditions.

In our previous study (Chapter 1), tree stumps appeared to be positively associated with recruiting *Picea abies* saplings. Tree stumps were therefore considered as potential safe sites for tree regeneration in wooded pastures, enhancing saplings establishment and survival as following: (i) as obstacle for cattle, stumps are mostly avoided, offering safe growth conditions against browsing and trampling pressure (but see Kupferschmid & Bugmann 2005); (ii) by their elevated position, tree stumps provide favourable conditions as competition-free position above the surrounding herbaceous vegetation (Hornberg et al. 1997) and soon free of snow in spring and avoiding heavy snow loads over winter known to damage small tree saplings; (iii) the growth context of decayed wood is most probably favourable for positive mycorrhizal associations with *Picea abies* saplings (Weiss 1991, Gobl 1996, Phillips & Fahey 2006) and nutrient availability (Baier et al. 2006).

The aim of this chapter is to present briefly a study we achieved on the positive association of tree stumps and tree recruitment, a with the possible mediation effect of shrub species in the grazed context of wooded pastures of the Swiss Jura Mountains. In particular, the following hypothesis will be explored using a field descriptive method: (i) the presence of shrub species around stumps is positively associated with recruiting tree species; (ii) the presence of thorny shrub species increases the probability of tree recruitment in shrub patches.

Methods

Study site

From a preliminary inventory of wooded pasture sites of at least one hectare size within an area of 30 km over the Swiss Jura Mountains, twelve study sites were selected according to a stratified random selection, based on altitude and average tree cover. Two altitude levels were defined: (i) low altitude, from 650 to 850 meters a.s.l. and, (ii) medium altitude, from 850 to 1100 meters a.s.l., as well as three levels of mean tree cover: (i) scarcely wooded pasture, with less than 20% tree cover, (ii) moderately wooded pasture, with tree cover ranging between 20 and 50% and, (iii) densely wooded pasture, with tree cover ranging between 50 and 70%. For each altitude – tree cover level combination, two sites of at least one hectare were chosen, with the condition to host at least ten tree stumps, in total twelve sites (see detailed site description in Table 1). In each study site, ten tree stumps were randomly selected for further investigations, representing a total number of 120 stumps for this study.

Table 1: Description of the twelve study sites, in which ten tree stumps were randomly selected for further investigations on shrubs and recruiting tree species.

Site	Location	altitude	tree cover	surface	mean slope	orientation
		LOW ALTITUDE SITES (650 - 850 meters a.s.l.)				
Corgémont (BE)	7°08'E, 47°11'N	670 m a.s.l.	0 - 20%	1 ha	30%	E
Courtelary I (BE)	7°05'E, 47°10'N	750 m a.s.l.	0 - 20%	2.5 ha	60%	SE
Cormoret II (BE)	7°02'E, 47°10'N	720 m a.s.l.	20 - 50%	1 ha	25%	NW
Cormoret III (BE)	7°02'E, 47°09'N	730 m a.s.l.	20 - 50%	1 ha	15%	SE
Courtelary II (BE)	7°05'E, 47°10'N	750 m a.s.l.	50 - 70%	1 ha	45%	SE
Cormoret I (BE)	7°02'E, 47°10'N	750 m a.s.l.	50 - 70%	1 ha	20%	NW
		MEDIUM ALTITUDE SITES (850 - 1100 meters a.s.l.)				
La Corbatière I (NE)	6°49'E, 47°04'N	1100 m a.s.l.	0 - 20%	4 ha	10%	NW
Creux-des-Biches (JU)	7°01'E, 47°15'N	1000 m a.s.l.	0 - 20%	1 ha	0%	NW
La Corbatière III (NE)	6°49'E, 47°04'N	1080 m a.s.l.	20 - 50%	1 ha	30%	SW
Saignelégier (JU)	7°01'E, 47°15'N	990 m a.s.l.	20 - 50%	1 ha	15%	SE
La Corbatière II (NE)	6°49'E, 47°04'N	1100 m a.s.l.	50 - 70%	1 ha	35%	SW
Cerneux-Joly (JU)	6°56'E, 47°12'N	1000 m a.s.l.	50 - 70%	1 ha	20%	NW

Data collection

For each tree stump, the surrounding vegetation was recorded, focussing on tree and shrub species. Within an circular area of 4 meters radius centred on the stump, a vegetation survey was performed for shrubs, including a species list and the visual estimation of the percentage absolute cover for each species using the dominance codes of Braun-Blanquet (Braun-Blanquet 1964). Cover scores were converted to percentage median values for further calculations. Additionally, a height dominance index was recorded for each species, which is a visual estimation of the average height of the foliage to the nearest 50 cm above the ground surface. The absolute cover value was then multiplied by the height dominance index, giving a volumic dominance value for each species, interpreted as an estimate of the relative biovolume occupied by each species within the plant community.

In order to interpret the vegetation dynamic in a synthetically, tree species were grouped into three cohorts according to the species colonization strategy derived from Rameau (1987, 1993): (i) pioneer tree species, fast-growing, with short-life ability to colonize open areas: *Sambucus racemosa*, *Sorbus aria*, *Sorbus aucuparia* and *Sorbus mougeotii*; (ii) post-pioneer species, slow-growing and of medium-longevity: *Acer pseudoplatanus*, *Corylus avellana*, *Fraxinus excelsior* and *Prunus avium*; and (iii) dryad species, slow-growing, shade-tolerant and long-lived: *Abies alba*, *Fagus sylvatica* and *Picea abies*. Finally, shrub species grouped into thorny species including *Rubus* and *Rosa* species, *Crataegus* species and *Prunus spinosa*, and thorn-less species including *Rhamnus catharticus*, *Viburnum lantana*, *Lonicera xylosteum*, *Lonicera nigra* and *Ribes* species, according to literature.

Around each stump, the following environmental descriptors were collected: (i) the total potential sun hours (further named PS_{hours}) over the vegetation period (May to October) measured using a solar compass (Herzog Forsttechnik AG, Switzerland), in order to estimate the shading effect of the neighbouring trees; (ii) the slope derived from horizontal distance and vertical elevation measures; (iii) the number of shrub patches in the neighbourhood of the stump at a distance ranging between 4 and 15 meters.

Data analysis

In order to investigate the relation between the shrub species and environmental descriptors, a Canonical Correspondence Analysis (CCA) was carried out on the shrub biovolume data with a Hellinger transformation (Legendre & Gallagher 2001), constrained by the standardized environmental matrix. Shrub species with a frequency below 5% were removed of the analysis.

For a further interpretation of the association between shrub and tree species around stumps, a Redundancy Analysis (RDA) was achieved on the presence-absence of tree species from each of the three species strategy groups, constrained by the presence-absence of thorny and thorn-less shrub species, in addition to stand tree cover and number of shrub patches within the next 15 meters. On both constrained analyses, an ANOVA like permutation test under the reduced model was performed with 999 permutations to test the significance of the overall model (Legendre and Legendre 1998).

Constrained ordinations and permutation tests were preformed using cca, rda and permutest.cca functions of the vegan library in R 2.4.0 (R Development Core Team 2006).

Results

On the 120 sampled tree stumps, 23 were found to be without any shrub species within a radius of 4 meters, whereas tree species were found on 70 stumps, 6 times without shrub species. Tree species were represented by *Picea abies* (34 times), *Fagus sylvatica* (14 times), and *Abies alba* (3 times) for dryad species, *Acer pseudoplatanus* (25 times), *Corylus avellana* (16 times), *Fraxinus excelsior* (8 times) for post-pioneer species, and *Sorbus aucuparia* (35 times), *Sorbus mougeotti* (5 times) and *Sorbus aria* (4 times) for pioneer species. Among shrub species, *Rubus* sp. pl. and *Rosa canina* were the most frequent thorny species (45 times; 35 times), and *Lonicera xylosteum* the most frequent thorn-less species (38 obs.).

Despite the low variance proportion represented by the reduced model in the CCA of the tree and shrub species, the gradient combining altitude and PS_{hours} discriminated species along the first ordination axis (Figure 1). At at medium altitude (850 – 1100 m a.s.l.), *Acer pseudoplatanus* was frequently surrounded by *Rosa pendulina*, *Sorbus aucuparia* and together with *Fraxinus excelsior* (Figure 1). At low altitude (650 – 850 m a.s.l.), *Corylus avellana* was often found together with *Prunus spinosa*, *Salix* and *Crataegus* species. *Picea abies* did not show a clear discrimination in relation with the recorded environmental descriptors, while *Fagus sylvatica* appeared under low PS_{hours} and preferentially on slope stands. On stumps situated in open areas, far form neighbouring trees and under high PS_{hours}, *Ribes* species and *Rosa canina* were frequent. On the other hand, under the influence of surrounding trees (i.e. low PS_{hours}), *Acer pseudoplatanus* was frequently found together with *Fagus sylvatica*, *Viburnum lantana* and *Lonicera* species (Figure 1).

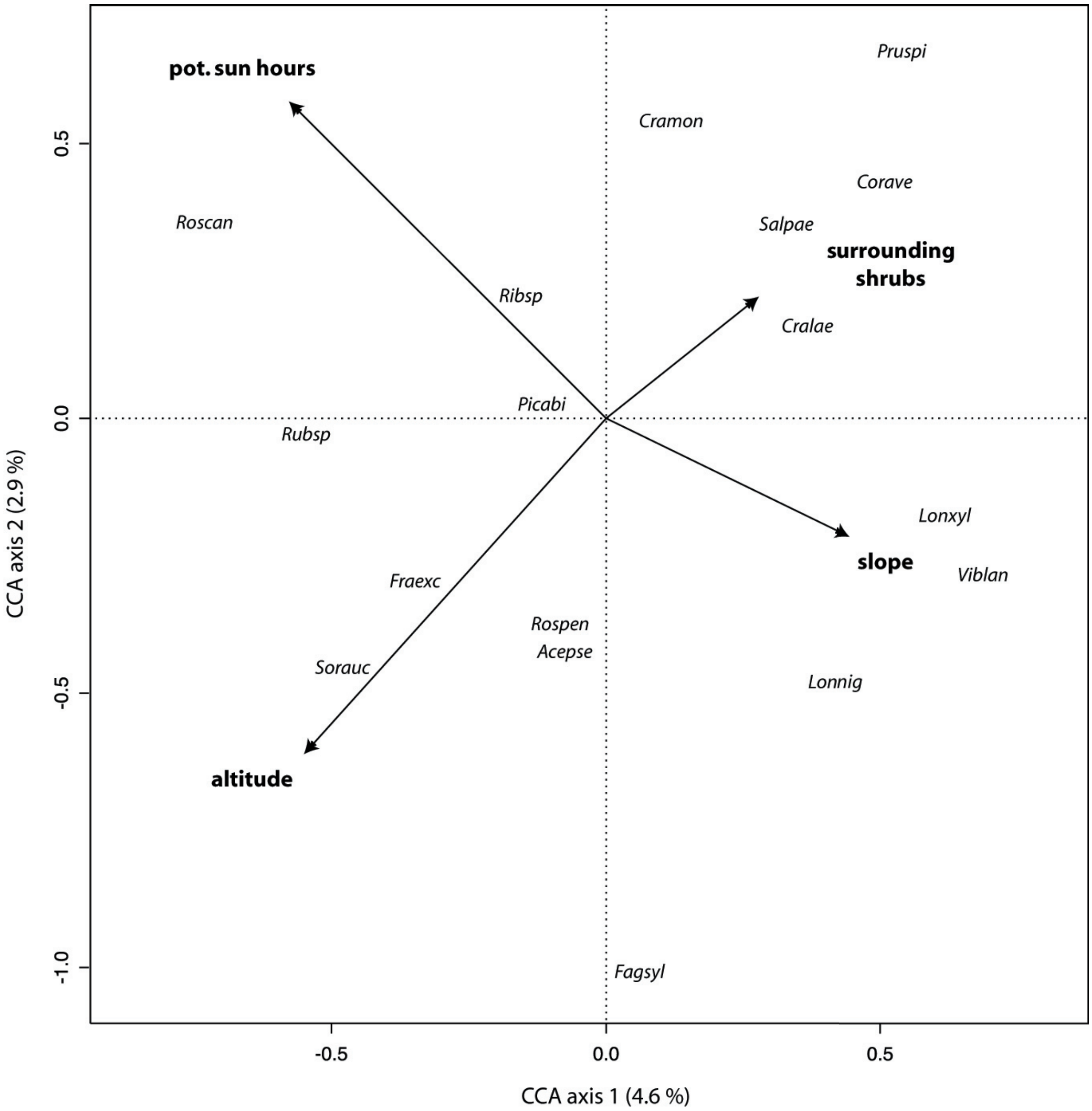

Figure 1: Canonical Correspondence Analysis of the tree and shrub species (biovolume) constrained by environmental descriptors. Species data were transformed with Hellinger (Legendre and Gallagher 2001) and environmental variables standardized. Total variance: 4.587; variance described by constrained axes: 0.414 ; result of ANOVA-like permutation test: P < 0.001; scaling type 2; n = 120. Acepse = Acer pseudoplatanus; Corave = Corylus avellana, Cralae = Crataegus laevigata; Cramon = Crataegus monogyna; Fagsyl = Fagus sylvatica; Fraexc = Fraxinus excelsior; Lonnig = Lonicera nigra; Lonxyl = Lonicera xylosteum; Picabi = Picea abies; Pruspi = Prunus spinosa; Ribsp = Ribes species; Roscan = Rosa canina; Rospen = Rosa pendulina; Rubsp = Rubus species; Salpae = Salix species; Sorauc = Sorbus aucuparia; Viblan = Viburnum lantana.

The RDA analysis of the presence of tree saplings in relation with the surrounding tree cover and the occurrence of thorny shrub species showed first that the presence of tree species was related to the occurrence of shrubs, the site tree cover contributing positively as well (Figure 2). Pioneer tree species appeared to be positively associated with thorny shrub species, whereas the relation thorn-less shrubs and surrounding trees was mostly related to post-pioneer and dryad tree species. On the other hand, the absence of tree species was associated with the absence of shrubs, were they thorny or not.

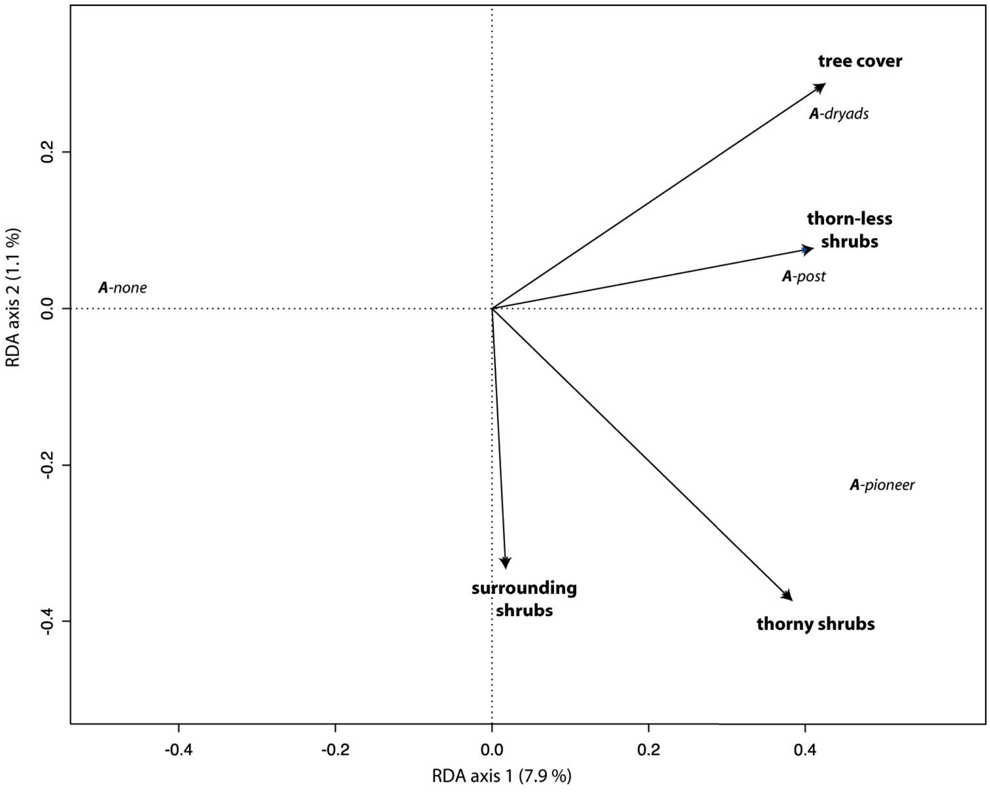

Figure 2: Redundancy Analysis on the presence of tree saplings according to their growth strategy, constrained by the presence of thorny and thorn-less shrubs, site mean tree cover (tree cover) and the number of shrub patches within the next 15 meters around the tree stump (surrounding shrubs). Total variance: 0.944; variance described by constrained axes: 9.5%; result of ANOVA-like permutation test: P = 0.002; scaling type 2; n = 120. A-pioneer = pioneer tree species; A-post = post-pioneer tree species; A-dryads = dryad tree species; A-none = absence of tree species.

Discussion

Despite the low proportion of the total variance displayed in the reduced space of the CCA computed on species biovolume constrained by the environmental descriptors, some interesting trends appeared in our results. The ecological gradients of light availability due to the shading effect of neighbouring trees, altitude and the vicinity of other shrub patches display meaningful species association in relation with their ecological requirements. Further ecological interpretations would indeed require a more extensive survey of environmental conditions, including orientation, topography, intensity of cattle trampling and browsing pressure and edaphic properties. Further comparisons with already described shrub communities found in wooded pastures would be meaningful as well, but overpasses the aim of this brief study.

Indeed, the attempt to analysis the presence of tree species in relation to shrub species and their defence traits displayed interesting gradients. They support the idea that the presence of shrubs contributes to tree recruitment in wooded pastures, even on tree stumps, and confirm in this sense our first hypothesis. Furthermore, the positive association between thorny shrubs and pioneer tree species indicates that those shrubs most probably play a protective role against browsing by cattle, which confirms our second hypothesis. But those results would require further support especially from an architectural community analysis and the comparison with surrounding shrub communities not under the influence of decaying stumps.

Assuming the natural tree species succession from fast growing pioneer species which are able to colonize open areas to post-pioneer and further to slow-growing shade tolerant dryad species, the presence of thorny shrubs seems to initiate a succession leading at the final stage to a new forest patch dominated by *Picea abies* and/or *Fagus sylvatica*. After the establishment of the first tree pioneers such as *Sorbus aucuparia*, the presence of thorn-less shrub species contributes further with the already established species to the recruitment of the post-pioneer species *Corylus avellana*, *Acer pseudoplatanus* and *Fraxinus excelsior* as possible obstacle protecting against cattle pressure. The dryad species *Picea abies* and *Fagus sylvatica* will then follow in the succession. Balancing the possible competition for light and space within shrub communities, their structure contribute in favourable conditions for further recruiting tree species through associational resistance.

Concluding, stumps remaining from logged trees often constitute the initial point of the new woody species succession from shrubs to dominant tree species, thorny shrubs positively contributing in the progress of the succession in the grazed context of wood pastures. Further investigations should hence be undertaken for further support of these conclusions, focussing especially on a temporal analysis of the succession in the establishment of woody species using dendro-ecological analysis, and the detailed comparison between shrub communities on decaying stumps and neighbouring shrub patches. Wooded pastures above 1100 meters a.s.l., known to host scarce shrub communities, should be investigated as well. In those conditions especially, an isolated tree which would have been cut may be hard to replace. Finally, a closer focus should be set on the reestablishment of grassland species in relation with the past understorey context, for a possible support of the shifting mosaic theory developed by (Olff et al. 1999) in grazed woodlands.

Acknowledgements

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DISCUSSION
&
SYNTHESIS

Introduction

Main objectives of my PhD study

The main objective of my PhD was to investigate the conditions allowing natural recruitment of *Picea abies* in wood pastures of the Jura Mountains. To this end, I focused on the successive live stages of tree saplings and used descriptive field approaches in order to identify survival and growth patterns, and further suggest relevant processes underlying natural tree recruitment.

My first objective was to determine whether established tree saplings were spatially associated with potential nurse structures, such as shrubs, tree stumps, rock outcrops and unpalatable plants, as predicted by the associational resistance hypothesis (Chapter 1).

Secondly, I investigated whether local plant communities as a whole, rather than individual unpalatable species, enhance tree recruitment in wood pastures after accounting for local environmental conditions, testing the following hypotheses: (i) at a given site and at an observation scale of 1 m^2, tree recruitment is dependent on the local plant community, even after accounting for the effect of local environmental conditions and individual unpalatable species with facilitative effects; (ii) the balance between positive and negative interactions may change for a given species depending on overall site conditions and history; (iii) different species could play the same facilitative role depending on the site (Chapter 2).

Thirdly, I treated the aspect of scale in facilitative interactions and tested the hypothesis of a scale dependency of the positive *vs.* negative association between saplings of *Picea abies* and the neighbouring plant species, in relation with species morphological traits (Chapter 3).

After that, I tested in the fourth part of my PhD the effect of presence and abundance of shrubs on the recruitment of tree species, and the fact that neighbouring trees can play the role of facilitative structures for tree saplings, in particular when no other nurse structure offers protection against cattle browsing (Chapter 4).

Then, in order to investigate the direct effect of cattle on *Picea abies* growth due to browsing impact, I proposed an original none-invasive method to investigate past height growth of *Picea abies* trees, as well as some results and perspectives it offers for further investigations (Chapter 5).

Finally, the perspective of a possible support for the shifting mosaic theory (Olff et al. 1999) led us to a brief investigation on the positive association of tree stumps and *Picea* tree recruitment, a with the possible mediation effect of shrub species (Chapter 6).

Main results

Tree recruitment was rather sparse in wood pastures under active agricultural and forestry pratices. The observation of the juvenile stages in a natural context was difficult. The few small trees seen above the herbaceous layer represented the small emerging part of a complex story taking place in the shade of the herbs. Definitively, the most crucial phases for tree establishment were hidden and under the influence of multiples interacting forces.

Our results showed that small *Picea* saplings (up to 40 cm) were positively associated with nurse structures such as rock outcrops, stumps, shrubs, low tree branches (Chapter 1). This suggested that those structures constitute safe sites for tree recruitment. In a competitive and grazed herbaceous context, the survival of saplings was further enhanced when associated with unpalatable species at the local scale of 4 m^2 (Chapter 1).

Furthermore in the herbaceous layer, far from shrubs and other neighbouring trees, where the exposure to light was better but also those to herbivores, the assemblage of plant species also contributed to better growth conditions for small *Picea* saplings, exempt from strong competition within the herbaceous layer and from high attractiveness for grazers (Chapter 2). In addition, *Picea* saplings were positively associated with shallow and sometimes alkaline soil conditions, which may influence both directly and indirectly above and below-ground competition for resources (Chapter 2). The investigations on the positive association between *Picea* saplings and the surrounding plant species assemblages at the smaller scale of one-dm^2 showed furthermore that the species-specific nature of the association vanishes in favour of an association with species morphological traits possibly closer to the underlying mechanism influencing saplings at this scale (Chapter 3). This characterized the surrounding plant community in direct relation with its ability to compete for light and nutrient resources, as well as to avoid attractiveness for grazers (Chapter 3).

At a broader scale, with a resolution of 25 m^2, and for a sapling height up to 1.5 meters, tree saplings were often associated with shrubs (Chapter 4). Within the shrub community, *Picea* saplings were most frequently associated with spiny species, which revealed their importance for tree recruitment under cattle pressure (Chapter 6). When shrubs were absent, the positive association occured between tree saplings and the canopy tree cover, revealing a possible self-enhancing effect of higher neighbouring *Picea abies* against the impact of cattle, despite conditions of potentially high intraspecific competition (Chapter 4). Low branches may therefore be an alternative nurse structure favourable for tree recruitment in wood pastures. Furthermore, the observation of the canopy tree cover and sapling recruitment patterns revealed multi-scale structures, probably resulting from the hierarchical integration of numerous interdependent processes over time and scale (Chapter 4).

On *Picea* saplings of increasing size, the constraints are changing, as they are now visible above the grassland context out of which it escaped successfully. Progressively, further successful survival requires another adaptive strategy in response to the changing constraints. *Picea* saplings displayed a height-threshold at around 1.5 meters, below which both height and lateral growths were reduced whereas branchiness and wood/leaf ratio increased. Such a growth pattern may reflect a strategy of resistance against browsing by cattle (Chapter 5). Above this height-threshold, suppression of lateral and height growth was released, and the tree displayed a compensatory growth pattern up to 2.3 meters height. This suddenly increasing growth rate may possibly be due to a well-developed root system, whose growth might not have suppressed by the above-ground browsing pressure. It will allow these trees to reach the adult status within a short time (Chapter 5).

Natural death of mature trees occurs scarcely in wood pastures according to personal observations, but precise data on tree mortality are yet missing. As a man-made landscape, the wood pastures require the disturbance through occasional tree harvesting for their maintenance. Once adult trees are cut, the remaining stumps, usually left on place, constitute a new structure in a suddenly open space. *Picea* saplings were found to be positively associated with such stumps because they provided a safe environment (Chapter 1) and enhanced tree recruitment in combination with the development of a shrub community (Chapter 6). Here again, the association with thorny shrub species revealed their potential function interfering between tree recruitment and cattle browsing pressure (Chapter 6).

In conclusion, if *Picea* saplings do have enough time to survive despite their low growth rate and large biomass ratio invested into leaves, they reinforce their below-ground position and develop an adaptive shape which protects their shoots against browsing. The survival as juveniles and resistance to browsing allowed *Picea abies* to become such a dominant species in the wood pastures of the Jura Mountains. The constraining and changing environment along several ecological axes requires for *Picea* saplings the ability to 'wait', to survive and possibly to develop adaptive responses. Our results contribute in better defining the 'place' of the successive live stages of *Picea* trees within their environment in the silvo-pastoral system. In other words, it tells us something about the ecological niche of *Picea abies* in the ecosystem of wood pastures.

Where is the niche ?
Integration into the ecological niche concept

In ecology, the definition of the term 'niche' is a continuing source of confusion and has been neglected by plant ecologists over the past decade (Chase & Leibold 2003, Laland & Sterelny 2006). Following the words of Lachaise (1979): «Sixty years of controversy, without any unified definition yet raised, what a poor result for this concept in ecology. However, its hard life over decades must reveal the strong theoretical necessity for such a concept in ecology». Grinnell (1917), at first, defined the niche as the unit of habitat a species occupies, based on the physical and climatic conditions that allow the species' life. Focussing on the role species play among others in relation to food and enemies, Elton (1927) came to a more functional definition of the niche term: the 'place' in a biocenosis where a species could find food and escape from enemies. This trophic definition of the ecological niche led consequently to the modern niche concept initiated by Hutchinson (1957).

The modern niche concept is defined by the conditions and resources needed by an individual or a species in order to practice its way of life, including both abiotic and biotic factors (Hutchinson 1957). It results in a synthesis of tolerances and requirements in as many dimensions as there are ecological factors being once limiting or determinant along the life span of an individual. The niche is therefore considered to be an *n*-dimensional hypervolume called the niche space (Silvertown 2004), where *n* is the number of dimensions making up the niche. There is no a priori method to detect the right niche axes to study (Silvertown & Law 1987) and failure to detect a partition axis between coexisting species does not necessarily indicate the absence of such an axis (Silvertown 2004). The capacity of organisms to construct, modify, and select important components of their local environment is a process known under the term of niche construction (Day et al. 2003), being a potential evolutionary agent affecting both ecological and evolutionary patterns (Laland et al. 1999).

Contradictory debates raised from the alternative unified neutral theory developed by Hubbell (2001). In this theory, he makes the assumption of species equivalence in their responses to all constraints. Thus, species have no interspecific tradeoffs (Bell 2000, 2001), and random processes determine species assemblages within communities (Whitfield 2002, Gaston & Chown 2005). The further stochastic niche theory developed by Tilman (2004) resolves partly this divergence, including stochastic processes in the classical trade-off based niche theory. According to the stochastic niche theory, invading species become established only if propagules can survive stochastic mortality while growing to maturity on resources left unconsumed by already established species (Tilman 2004). Moreover, recent modelling results demonstrate that niche and neutrality may form ends of a continuum from competitive to stochastic exclusion (Gravel et al. 2006), whereas Leibold & McPeek (2006) argue that co-occurrence of similar or equivalent species is not incompatible with the niche theory, as niche relations may sometimes favour species coexistence. Temporarily concluding, it is time, following the opinion of Silvertown (2004) and Laland & Sterelny (2006), for the niche to be rehabilitated among ecologists, assuming indeed its possible limitations due to interdependent, unfixed and possibly catastrophic species response curves in relation to ecological factors (Frontier et al. 2004). And neutral perspectives may possibly be incorporated in a synthesized view as Leibold & McPeek (2006) suggested.

In the case of *Picea abies* in wood pastures, the recruitment phase is the most determinant one for the accomplishment of its life cycle. During the life-cycle of *Picea abies* in wood pastures, the most critical stages for an individual's survival is germination, seedling survival during the first year, survival and growth of the sapling within the herbaceous layer, and further above until overtopping in height the browsing pressure of cattle. Our results provide some insights into ecological constrains and adaptive responses for the two last phases, according to the main objectives of this study. The particular highlight on the regeneration niche *sensus* Grubb (1977) may help us understanding how *Picea abies* is able to coexist with other plant species and how it differs from others. In the regeneration niche concept, Grubb focuses on the component of the niche that is concerned with processes of such as seed production and germination and by which one mature individual is replaced by another (Grubb 1977). Our results allow us to identify some determinant ecological dimensions of the niche of *Picea abies*, defining in particular its the regeneration niche in a grazed context. Next, I will discuss it over the three main components of the niche which are habitat, trophic and temporal aspects, in order to propose as synthesis a conceptual model for the regeneration of *Picea abies* in wood pastures.

Abiotic environment as habitat component of the niche

A common vision on suitable environmental conditions for life includes appropriate habitat conditions, including abiotic resources required for survival, growth and reproduction. The abiotic niche of plant species is characterized by at least three important components. First, abiotic resources, such as space, water, light, and nutrients are required along the whole life-cycle. Second, co-occurring organisms may affect the availability of abiotic resources either by competing for similar resources or benefiting from positive synergisms like facilitated resource uptake. Finally, the available space and ensuing heterogeneity offer the physical place with the necessary variability for consequent resource supply. Grinnells' niche conception (Grinnell 1917) corresponds essentially to this habitat component of the ecological niche. In the case of *Picea* saplings in wood pastures, space, microtopography, rock outcrops, mean soil depth, and physical obstacles such as stumps, shrubs and low branches, possibly interacting with biotic components of the niche related in particular to herbivores and below-ground communities.

Biotic interactions contributing to a 'social' niche

The place of an organism in the environment in relation to its food and the consumers that prey upon it defines the trophic niche (Odum 1971, Silvertown 2004). It sets species within the trophic structure of ecosystems, unfolded in food networks (Higashi et al. 1992). The trophic niche, which can be easily conceived for animals feeding on a high variety of foods, appear less obvious for plants living basically on a small set of resources such as CO_2, light, nitrogen, phosphorus, potassium and a common set of mineral nutrients (Silvertown 2004). Interspecific competition for these few same resources is the norm in plant communities (e.g., Goldberg & Barton 1992), highlighting the role of interactions with other organisms as important component of a plant species' niche.

Interspecific interactions, in a balance between competition and facilitation, could be included as components of the trophic niche, implying biogenic relations among organisms. Self-enhancement, balanced by intraspecific competition for common resources and by a possible allelopathic effects could also be included in the extension of the trophic niche. Finally, an additional component of the niche could be the number of individuals co-occurring in a given patch, as with an increasing number of individuals present, the level of intraspecific competition increases and each individual's risk of being consumed by predators or herbivores decreases.

In the case of *Picea* saplings in wood pastures, the direct browsing and possibly trampling pressure by cattle, the probable sapling-mycorrhizae synergisms enhanced by decaying wood and further edaphic conditions, and the competitive-facilitative interactions with neighbouring species belong to the biotic component of the niche, mostly as a result of indirect interactions.

The niche is temporal

Limiting resources may be structured in space and/or time, which results in a temporal differentiation between the species due to an underlying differential resource utilization (Loreau & Ebenhoh 1994, Nilsson et al. 1996, Chesson & Huntly 1997, Chesson 2000). The synchronic and successive combination of favourable niche conditions is therefore required along the different life stages over time and space to insure survival and reproduction and temporal niche differentiation may promote coexistence with other regeneration phases and other species in a dynamical way (Chesson 1991, Chesson & Huntly 1997).

In our case, the grazing period and frequency, in relation to the vegetation and tree seasonal growth, as well as the position of the other niche components on the life cycle of *Picea* trees (i.e. position in time, related to above- and belowground growth) belong to the temporal component of the regeneration niche of *Picea abies* in wood pastures.

Ontogenetic shifts makes the niche dynamic

For most organisms, ecological requirements change along their life cycle. Assuming the ecological niche concept, it means changes in niche breadth and/or position during the life of individuals. This dynamical process is called ontogenetic niche shift (Parrish & Bazzaz 1985). Unable to seek actively for ideal habitats, plants display distinct tolerance levels to extrinsic factors at their different developmental stages (Turner et al. 1969, Franco & Nobel 1989, Lyons & Barnes 1998). Although it has received little attention (but see Miriti 2006), the ontogenetic niche shift concept provides a useful framework for a better understanding of responses of juvenile and adult plants to spatial and temporal variability.

In the context of tree regeneration, the drift of environmental conditions is necessary in order to remain most favourable over the successional phases of tree recruitment, from seed arrival to an emerged tree reaching the canopy of the forest subsystem of wood pastures.

Wood pastures live on permanent disturbances due to cattle activity, and occasionally on farmer or forester interventions, in combination with the natural vegetation succession dynamic which would lead back to a forest climax. Resulting patterns and processes, highlighted especially for plant communities (Bokdam & Gleichman 2000, Kohler et al. 2004, 2006a), were highly dynamical, revealing an unstable equilibrium of a system living on intermediate disturbances (Roxburgh et al. 2004). The ability of adaptation to the initial perturbation and its consequences is therefore crucial for survival, and organisms such as plants who are mainly unable to move around have to be at the right place since the beginning.

Picea abies showed in our study how survival is possible under permanent competitive pressure from neighbouring plant, taking sometimes the advantage of positive associations, before developing an adaptive growth shape in order to resist over time on the browsing impact. Those transitions between growth stages result in abrupt ontogenetic transformations and niche shifts (Loreau & Ebenhoh 1994).

As for many other ecosystems, perturbation is a guarantee for the wood pasture system to be alive and maintained (i.e. processes running between sources and sinks of the system). Flood plains, shrublands, agricultural landscapes, and inter-tidal landscapes belong for example to those ecosystems living on disturbances (Paine & Levin 1981, Selinger-Looten et al. 1999, Tilman 1999, Hooper et al. 2005). Species taking advantage of disturbances are nowadays often the most successful ones, promised to the nicest future in the world of more and more constrained nature. The success-story of *Picea abies* in the Jura Mountains and especially in wood pastures relies on its ability to live under disturbance.

A conceptual model of tree regeneration in wood pastures

Our work allowed us to elaborate a conceptual model of tree recruitment and growth in wood pastures (Figure 1), integrating the results of the present study and further knowledge from literature and previous research projects. Our model is structured along the life cycle of the tree, distinguishing the following life stages:

Picea as a seed

Presence and viability of seeds are the first requirement for possible tree recruitment. Seed abundance and distribution depends on the proximity to mature trees, on the dispersal mode and on possible tapping structures

(Johnson & Fryer 1992, Clark & Ji 1995, Wijdeven & Kuzee 2000, Hewitt & Kellman 2002). Little information is available for *Picea abies* on seed rain abundance, frequency, and spatial distribution, as noted by Ammer et al. (2002) (but see Hofgaard 1993). In the wood pasture context, the importance of a seed trapping effect by small shrubs has been nuanced by Smit (2005). Germination rate is affected by microclimate conditions such as moisture and light (Desteven 1991, Berkowitz et al. 1995, Brang 1998, Losvik 1999, Béguin 2001, McAlpine & Drake 2003), by the germination substrate (Fleming & Mossa 1994, Oleskog & Sahlen 2000, Béguin 2001, Mori et al. 2004) and the impact of seed predation (Desteven 1991, Wenny 2000, Cote et al. 2003), as well as indirectly by microtopography (Gunnarsson & Hakan 1998, Kuuluvainen & Juntunen 1998) and the surrounding vegetation (e.g., Isselstein et al. 2002). However, the influence of both surrounding vegetation and microsite characteristics on suitable microclimatic conditions for seed germination remains partly unknown (but see Hornberg et al. 1997, Isselstein et al. 2002). In wood pastures, Vandenberghe et al. (2006) showed for *Picea abies* seeds a low germination rate (17%) compared to *Acer pseudoplatanus* and *Fagus sylvatica*, and an increased germination rate due to gap occurrence and size within the herbaceous layer (Vandenberghe et al. 2006).

Picea seedling (first year)

From germinated seeds raises a seedling whose fate will depend further on microclimatic conditions such as humidity and light availability, as well as on nutrient uptake and the neighbourhood of adequate mycorrhizae (Andre et al. 1987, Andre 1994, Gobl 1996, Bonkowski et al. 2001). Biotic environmental factors seem to contribute progressively to the definition of the regeneration niche of *Picea abies*.

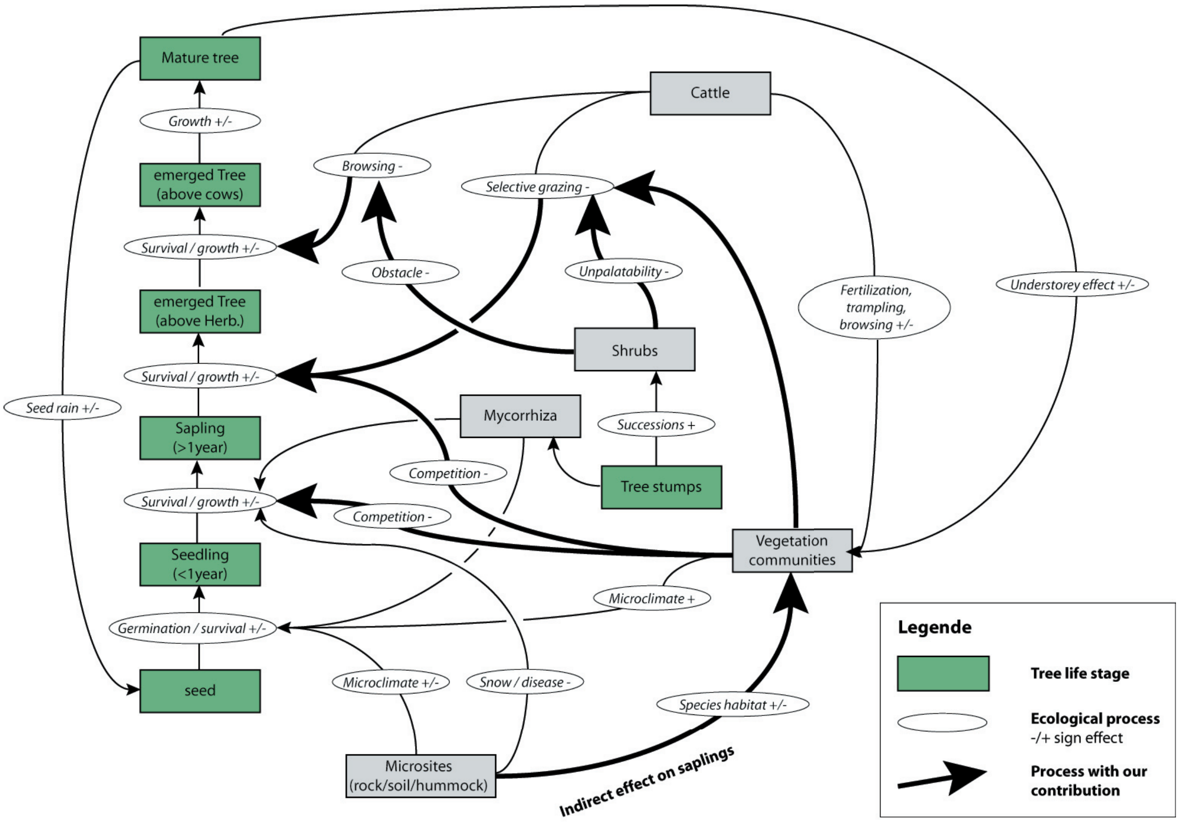

Figure 1: Conceptual model of the regeneration and growth of Picea abies in wood pastures (see text for details).

In our study, we focussed on young *Picea* trees after their first growing season because if they could be found alive after their first year, we could assume that the actual surrounding conditions allow at least their survival. Furthermore, this focus potentially reduced the contribution of randomness in the location of tree recruitment, the effect of the successive ecological filters on the previous stages being integrated in the picture of the remaining tree recruitment at a given stage.

Picea sapling among herbs

At this stage, *Picea* saplings grow within the herbaceous layer, competing with neighbouring plants for light and space, both above and below ground, as well as for nutrient supply (Lautenschlager 1999, Bolte & Villanueva 2006). Morphological traits of the surrounding species, in particular the ability for vegetative spread and competitiveness will affect sapling survival (Chapter 3).

The herbaceous vegetation being grazed selectively by cattle, its species composition will contribute through its pastoral value to the chances to be grazed or not. As tree saplings are individually undistinguishable for cattle selectivity within the herbaceous vegetation, they may only be grazed by chance, together with attractive herbs. In case of direct browsing, small *Picea* saplings (10-15 cm) showed lower survival compared to broadleaf species such as *Fagus sylvatica* or *Acer pseudoplatanus* (Vandenberghe et al. 2007), plausibly because *Picea* stores a higher proportion of biomass in leaves and raising slower out of the herbaceous layer than saplings of broadleaf tree species, due to its above-ground architecture. The duration of this phase is about 3 to 5 years, but depend highly on environmental factors influencing sapling growth.

Picea sapling among cattle

Slowly growing in height, *Picea* saplings will progressively extend their root system and consolidate their establishment if survival is possible (Gobl 1996, Puhe 2003), being progressively more resistant to unfavourable conditions and occasional disturbances. Growth leads *Picea* saplings to emergence from the herbaceous layer and be directly affected by browsing caused by cattle. The intensity of the browsing damage on tree saplings seems to be linearly positively related to the stocking density (Mayer et al. 2006).

Neighbouring nurse structures such as rock outcrops, tree stumps, shrubs and other conspecific trees influence cattle behaviour and consequently become crucial for saplings survival, obstacles and repellent species leading to avoidance. There is evidence that defence traits of the neighbouring plants can influence the degree of protection of a *Picea* sapling, these associational effects depending on the spatial scale of herbivore selection (Bergvall et al. 2006). The adaptive growth *Picea* is able to develop under browsed conditions will further enhance significantly its survival chances, allowing its growth towards a mature seed producing spruce tree. The negative effect of intraspecific competition and allelopathic effects are most often not sufficient to balance the positive effect of associational resistance (Pellissier 1993, Souto et al. 2000).

Other key-components of the silvopastoral system will contribute or affect differentially each life stage, by direct or indirect effects (Figure 1):

Cattle through their behaviour will affect *Picea* saplings directly by selective grazing and browsing, and will influence the herbaceous plant communities by fertilizing, trampling and removing biomass (Kohler et al. 2004). On the other hand, cattle behaviour will be driven partly by topographical conditions, site configuration and vegetation attractiveness (Kohler et al. 2006b).

More abundant in wood pastures of lower altitude and partly avoided by cattle, *shrubs* will prevent *Picea* saplings being browsed, because they are an obstacle or, in case of spiny species, because they are a mechanical defence. The establishment of shrub species seems to be enhanced in particular by tree stumps, which probably reflects a natural succession of pioneer vegetation (Kohler 1999), benefiting of the stump as an obstacle being surrounded by species of low interest for herbivores, and of the nutrients newly released by the litter decomposition (Douard 1994).

Tree stumps themselves may enhance survival and growth of *Picea* saplings, as already shown in other studies (e.g., Purdy et al. 2002, Gronli et al. 2005). They offer a favourable growth context, so that the sapling soon grows higher than potentially competitive neighbouring plants and than the remaining snow cover in spring. Furthermore, decaying wood offer favourable conditions for mycorrhizal communities (Gobl 1996, Baier et al. 2006).

Mycorrhizae are associated at the root level with most of the vascular plant species, and play important and still mostly unknown functions in particular for nutrient uptake (Smith & Read 1997). Mycorrhizal associations have been shown to contribute in growth and survival of tree seedlings, being probably determinant for certain species including *Picea abies* (Carleton & Read 1991, Ponge et al. 1998, Zackrisson et al. 1998). The underlying role of mycorrhizae in both intra- and interspecific interactions implying *Picea* saplings in wood pastures was certainly underestimated. There contribution is most probably complex, involving competition and positive associations, as well as local below-ground soil conditions at the scale they operate. For sure, much remains to investigate in this field and its integration in further research will certainly contribute in a better understanding of observed vegetation patterns.

Finally, *vegetation communities* already driven by cattle activity will be further determined by habitat characteristics according to species requirements and tolerance. The framework made by the geological substrate, topography and edaphic conditions determines partly the processes we described as determinant for tree recruitment and growth, whereas standing trees themselves will have feedback effects on those vegetation communities and on microhabitat conditions (Douard 1994).

Concluding, from mostly being constrained as a juvenile, the tree slowly becomes constraining for its environment. In addition, the constraints on recruitment and growth of *Picea* saplings change in time and along the succession of life stages. This means that environmental conditions have to change along the life stages in order to remain most favourable to *Picea* sapling survival and growth. The additive effect of these numerous ecological filters acting as selection pressures precisely means ecological plasticity and an ontogenetic shift of the niche. Along the period of growth under multiple constraints, the niche possibly becomes narrower, and the contribution of randomness becomes lower as the tree grows and through the successive integration of all ecological filters.

Set back in the spatial mosaic structure of wood pastures, does such a shift of the niche conditions over time necessary lead to shifting mosaics over space?

To the global dynamic of the system (shifting mosaic hypothesis)

Over periods of several years, the replacement of plant developmental stages, species and communities leads to vegetation successions (e.g., Clements 1928, Burrows 1990). Is the series of stages, species or communities recurrent and ecologically linked, the succession becomes cyclic (e.g., Watt 1947, Miles 1979). Alternatively, the non-cyclic 'carousel' succession model (van der Maarel & Sykes 1993) rends the state of the site independent of the preceding dominant one (Herben et al. 2000) as no ecological link relates both status. Finally, patches passing through the phases of a cycle in a de-synchronized way defined shifting successional mosaics (Olff et al. 1999). According to the 'shifting mosaic' theory, internal plant processes (e.g., growth), vegetation processes (e.g, competition, facilitation) and external influences (e.g., herbivory, management) drive those successions over time and space: unpalatable plants facilitate the establishment of trees in open grasslands, which outcompete in turn their facilitators and reduce further tree recruitment in the neighbourhood so that grassland may reappear after trees die.

Evidences for mosaic ecosystem structures are numerous, but support a possible shift remains scarce. The importance of mosaic landscapes has been highlighted recently, the variety of scales, structures, substrates and processes providing a certain degree of freedom for species to move around in the landscape and hence maintaining biodiversity in the long-term (Segerstrom 1997, Waldhardt et al. 2003, Fuhlendorf et al. 2006). Shifting mosaic landscapes are often related to intermediate disturbance regimes (Linderman et al. 2006, Wimberly 2006). According to the intermediate disturbance hypothesis (Connell 1978, Huston 1979), small gaps acting as regeneration niches are permanently created, which can then be occupied by any one species of a guild according to priority as determined by proximity and establishment success (e.g., Kohler et al. 2006a).

In forest ecosystems, the species growth and turnover is particularly slow and the detection of shifting mosaic patterns not easy. Moreover, long-term data on species distribution and environmental changes are often missing. Several attempts were done to demonstrate the potential of this model in forest (e.g., Liu et al. 2005) and wooded pasture ecosystems (Rousset & Lepart 1999, 2000, Olff et al. 2000, Bakker et al. 2004, Kohler et al. 2005). Cyclic dynamics were stated by Bernier & Ponge (1994) in a mountain spruce forest, in relation to changes in humus forms and soil fauna. Bernier stated in particular that the tree growth phase was related to a shift of the humus form, from mull towards moder due to decline of earthworm populations. At a second phase which corresponds to the second half of the life of spruce trees, a humus form improvement was observed from moder towards mull humus due to a succession of earthworm species, in particular anecic ones (Bernier & Ponge 1994). At this stage, the establishment of *Picea* seedlings seemed to be favoured, in relation as well with the understorey vegetation (Ponge et al. 1998). Furthermore, Stocker (2001) concluded on the occurrence of shifting mosaic patterns with a turnover period of 325 +/- 25 years in a natural spruce forest of Central Europe. In further old-growth temperate forests, Busing (1998) showed alternatively that several tree species regenerate near conspecific adults, suggesting a limited mobility for such species within the shifting mosaic and contributing more to a steady state of the system.

In the case of tree regeneration in *Picea*-dominated wood pastures, the shifting mosaic theory has been implicitly supported by others (cf. NCCR PS6 project), without really going above the smart idea standing behind. It has been taken as a conceptual description of the system without describing first the system itself (e.g., Smit 2005, Vandenberghe 2006). The acceptance of the shifting mosaic theory for the dynamic of wooded patches within the wood pasture complex would mean for any location to be over time in the successive states leading from open grassland to a forest patch and back from the forest to the open grassland patch in a cyclic turnover in time and space. Looking at the current picture of the landscape, simultaneous succession phases neighbouring each other offer an indication for possible shifting mosaics. The mosaic is there, but does it really shift?

To assess a shift between patches of a mosaic, data over wide time span are ideally required. With insight into tree regeneration and growth, our results may however contribute indirectly to such an assessment, observed patterns and hypotheses on underlying processes providing some precious indications.

Whereas negative feedbacks (e.g., competition, predation) lead to stability, positive feedbacks (e.g., facilitation, self-enhancement), greatly underemphasized in community ecology, create ‘snowball’ effects, the phenomenon builds on itself becoming unstoppable (Gurevitch 2006). Compensatory, one-way facilitation (i.e. one species helps another but not reciprocally) reduces the potential ‘snowball’ effect (Gurevitch 2006).

Complex synergisms between positive feedbacks and other effects will drive the entire system over time and space.

Our results showed how tree stumps, usually left at place after tree harvesting, become again safe sites for tree regeneration, both directly (Chapter 1) and indirectly (Chapter 6). Stumps are furthermore most favourable to the development of shrub communities (Chapter 6); as these shrubs, especially spiny species, seem to have a protective function for tree saplings against browsing, they further enhance indirectly the recruitment conditions.

Whether the way back from a forested patch towards an open grassland is plausible remains highly uncertain. According to our results, we see two major reasons for it: (i) the positive association of *Picea* saplings with immobile rock outcrops contribute to a steady state of the forest patches over space, and (ii) tree stumps as hot spot for new tree recruitment contribute as well to the spatial stability. Furthermore, the soil conditions keep for a long time the memory of the understorey conditions (i.e. dry and with litter changing the soil biochemistry and understorey vegetation), the nutrients (especially nitrogen) released by the newly decomposing litter beginning a possible new evolution. The comeback of nutrient-poor grassland species therefore seems rather uncertain for us over the short term. Data have been collected in this sense (Iseli 2005).

Finally, the positive association observed in absence of shrubs between *Picea* saplings and mature trees (Chapter 4) will contribute to the spatial stability of the system, should it be a mosaic. The possible underlying self-enhancing feedback mechanism coupled with strong constraints beyond the current ecotone would either stabilize the woodland-grassland ecotone both spatially and temporally, as shown by Weltzin & McPherson (1999), and consistent with Wilson and Agnew's one-sided positive feedback switch hypothesis (Wilson & Agnew 1992).

Concluding, these results let us doubt of the real shift that would occur over space at the landscape scale in the pasture vs woodland mosaic of wood pastures in the Jura Mountains, according to the shifting mosaic theory developed by Olff et al. (1999). On this critical stage, human interventions may play a crucial role, removing continuously stones, shrubs and undesirable plant species such as unpalatable or species of low pastoral value. For us, stabilized mosaic patches result from the combined effects of tree recruitment, cattle behaviour, soil and geomorphological conditions, as well as management practices. Self-enhancement and positive association with stumps support spatial stability. Shrubs are the only possible pioneer step towards a possible shift, but nothing guarantees the come back to a grassland patch.

Perspectives

My PhD study contributed hopefully in a better understanding of regeneration patterns and processes of a highly dominant tree species in the fairly common and a priori unspectacular ecosystem of wood pastures. Banal species such as *Picea abies* often retain less attention among scientists, and I hope this study reinforced the conviction that behind common patterns stand complex and fascinating processes. Much was expected of this study, in relation with the ambitious purpose of an integrative ecosystem modelling perspective, promoted by previous studies and further research intentions (Gillet et al. 2002, Wagner et al. 2006, Buttler et al. submitted, Gillet submitted). At the time of its conclusion, interesting results emerged on a wide range of aspects, from local interactions between *Picea* saplings and surrounding plant species to association patterns at the landscape scale for example. It was possible to describe many patterns that I observed in the field, and to analysis their structure in order to reveal what may stand behind. Field studies have their intrinsic limitations of course, but much could be said at least about the possible underlying processes. However, it remains much to investigate in order to have a reasonable view on what happened around tree recruitment and its further feedback effects on communities of plants, insects and soil micro-organisms, in relation to disturbances at several scales, due to herbivores, management and climate.

Comparative studies on vegetation and recruitment dynamics in other semi-open landscapes structured by isolated trees, such as savannahs, boreal or alpine forests close to the tree line, would reveal possible invariant structures in functional and spatial patterns (Hester et al. 2006, Huth & Wagner 2006, Juntunen & Neuvonen 2006). Generalization of results would helpfully improve our understanding of these dynamical ecosystems, living mainly on intermediate disturbance regimes, and in which human activity and management implications are often high. In those ecosystems, furthermore, consequences of climate and environmental changes appear often at first, and a fine comprehension of patterns and processes will be crucial for their maintenance under changing conditions (Schroder & Seppelt 2006). Their integration probably constitutes one of the most important challenge for research and human activities in the future.

Further on, the question of the origin of these man-made ecosystems remains a challenging question addressed to current research. Are wood pasture landscapes in Central Europe remnants of European savannahs hosting big herbivores in the past? Until recently, primeval landscape , i.e. before any significant influence of man, was commonly considered as closed canopy forests, wood pastures thought to be derived from these primeval forests by the first Neolithic farmers (Pott & Hüppe 1991). In contrast, Vera (2000) proposed that primeval landscapes were not dominated by closed canopy forests but by wood pastures, kept open by now extinct large herbivores. According to Vera, domesticated animals gradually took the place of those large herbivores in their influence on the vegetation patterns. But recent paleoecological data let others doubt on the validity of this view (Mitchell 2005), and contributes to the ongoing debate (Birks 2005, Moore 2005). Concluding, the role of past disturbances and management choices on present patterns should be further investigated, and better taken into account as key aspect to deal with modern-day disequilibrium in ecosystems (Coomes & Allen 2007).

Finally, there is an urgent need for management tools and strategies based on current knowledge in ecology. Such tools should be well-adapted to people directly implicated in management choices and practices and be as simple as possible, but not too simple. Statistical modelling over space and time offer therefore promising issues and constitute essential approaches with a powerful integrative potential (Rammig et al. 2006, Wehrli et al. 2007, Gillet submitted).

Tree regeneration and growth will further shape diverse terrestrial ecosystems in the future, and much of this topic remains unexplored yet. Facing ecological complexity is challenging, let's do it further!

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