THE INFLUENCE OF CATTLE ACTIVITY ON TREE REGENERATION IN WOOD-PASTURES

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No one has yet described for me the difference between wild forest which once occupied our oldest townships, and the tame one which I find here today. It is a difference which would be worth attending to. The civilized man not only clears the land permanently to a great extent, and cultivates open fields, but he tames and cultivates to a certain extent the forest itself. By his mere presence, almost, he changes the nature of the trees as no other creature does….It has lost its wild, damp and shaggy look, the countless fallen and decaying trees are gone, and consequently that thick coat of moss which lived on them too…
Henry David Thoreau (1862)

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Looking back, I realise that my life has changed a lot in the last four years. During my PhD research and my life in Switzerland, I met plenty of lovely and interesting people that I would like to thank.

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I want to dedicate this work to the memory of my father, Paul Vandenberghe, who left us way too early and whom I miss so much. I carry you with me.

Summary

Wood-pastures are semi-natural, highly biodiverse systems maintained by traditional extensive agriculture. They are used for grazing and timber. The shifting mosaics of grassland, shrub thickets and woodland patches in these systems are driven by large herbivores. Current changes in agricultural practices are leading to either intensification or abandonment and they result in a segregation of grassland and forest. This presents a complex conservation problem for these endangered ecosystems. Large herbivores have been identified as an important factor preventing the establishment of trees and the regeneration of woodland. However, successful management is severely hindered by the lack of ecological knowledge about the effects of large herbivores on woody species.

This research focussed on the quantification of the impact of cattle activity on the early stages of tree establishment for four tree species (*Abies alba*, *Picea abies*, *Acer pseudoplatanus* and *Fagus sylvatica*) common in the wood-pastures of the Swiss Jura Mountains. Cattle can have both direct and indirect effects on tree establishment, and the interaction between cattle activity and both competition and facilitation by surrounding vegetation was studied. Experimental field studies (involving seed sowing and sapling planting) were carried out.

Both cattle activity and competition from neighbours reduced first-year tree seedling recruitment in wood-pastures. Seedling establishment decreased with increasing cattle grazing intensity. The effects of gaps in the vegetation on seedling emergence were complex, as a result of biotic (*i.e.* competition, facilitation and predation from rodents, invertebrates and large herbivores) and abiotic (*e.g.* moisture, temperature and light) interactions, leading to different results in different years. Although overall the chances for tree seeds to make it to seedlings were low, seedling establishment was relatively high for *Picea*, intermediate for *Abies* and *Acer* and low for *Fagus*.

The probability of a sapling of being browsed increased with sapling size and decreased with the height of surrounding vegetation and in the presence of nurse shrubs. It was similar for the four species and under low and high grazing intensities. Saplings had species- and size-specific responses in survival and growth to cattle browsing. Under both low and high grazing intensity, small coniferous saplings (36 %) had a lower survival rate than small deciduous saplings (53 %), which we hypothesize is due to the larger biomass losses stemming from a more vulnerable plant architecture. Under low grazing intensities, large *Picea* (80 %) and *Fagus* (67 %) saplings had a higher survival than large *Acer* (50 %) and *Abies* (33 %) saplings. This was likely due to differences in sapling tolerances to loss of biomass.

Simulated browsing damage resulted in relatively smaller growth losses when small saplings were growing slowly in the presence of neighbours. Shade increased this effect. At least in the short term, the degree of small sapling tolerance was not related to plant performance as saplings that compensated almost for biomass losses still had lower survival and growth rates than less tolerant saplings. *Picea* was the only species not negatively affected by strong irradiance as found in an open pasture.

For all tree species, the facilitative effect of nurse shrubs on small saplings was highest at intermediate levels of grazing intensity. Shrubs were more heavily damaged at high intensity than low intensity. Consequently, escaping browsing, sapling survival and growth was significantly increased by shrubs under low grazing intensity but not under high grazing intensity. Moreover, the positive effects of shrubs tended to be higher for coniferous species, and in particular *Picea* which was more sensitive to both competition from neighbours and browsing.

In conclusion, the resistance of trees to cattle activity varies among the early stages of tree establishment and is affected by tree species, grazing intensities and environmental conditions. Both competitive and facilitative interactions found between young trees and surrounding vegetation illustrate the complex nature of plant-plant and plant-animal interactions during the tree establishment phase in wood-pastures. The insight provided into the interactions between cattle grazing and tree establishment in wood-pastures will contribute to improve ecological theory and models, in addition to informing the management and conservation of wood-pasture systems.

Keywords: browsing, competition, conservation, ecosystem dynamics, facilitation, field experiments, grazing ecology, plantation, trampling, sapling survival, seedling emergence, seed sowing, Swiss Jura Mountains, tree diversity, tree establishment, tree species, resistance, sylvopastoral system, tolerance.

Résumé

Les pâturages boisés sont des écosystèmes semi-naturels abritant une grande biodiversité et sont maintenus par une agriculture traditionnelle extensive. Ils sont utilisés pour la pâture et l'exploitation du bois. Les mosaïques tournantes des pâtures ouvertes, des bouquets d'arbustes et des parcelles de forêts dans ces systèmes évoluent sous l'influence des grands herbivores. Les changements actuels dans les pratiques agricoles mènent à la fois à une intensification ou à l'abandon et il en résulte une séparation entre pâture et forêt. Ceci constitue un problème complexe de conservation pour ces écosystèmes menacés. Les grands herbivores ont été reconnus comme étant un facteur important limitant l'établissement des arbres et la régénération de la forêt. Cependant, une bonne gestion est sévèrement empêchée par des lacunes dans nos connaissances sur les effets qu'ont les grands herbivores sur les essences forestières.

Cette recherche a pour objectif de quantifier l'impact de l'activité du bétail sur les stades précoces de l'établissement des essences (*Abies alba*, *Picea abies*, *Acer pseudoplatanus* et *Fagus sylvatica*) communes dans les pâturages boisés du Jura suisse. Le broutage par les vaches peut avoir une action directe et une indirecte sur l'établissement des arbres, et l'interaction entre l'activité du bétail et, à la fois la compétition et la facilitation par la végétation herbacée a été étudiée. Des études expérimentales en champs (incluant des ensemencements de graines et transplantations de plantules) ont été réalisées.

L'activité du bétail comme la compétition avec les voisins herbacés réduisaient le recrû des semis d'arbres la première année en pâturages boisés. L'établissement des semis diminuait avec l'augmentation de l'intensité de broutage. Les effets des trouées dans la végétation sur l'émergence des semis étaient complexes, résultant des interactions biotiques (*i.e.* la compétition, la facilitation et la prédation par les rongeurs, invertébrés et grands herbivores) et abiotiques (*p. ex*. l'humidité, la température et la lumière), menant à des résultats différents suivant les années. Bien que, d'une façon générale, les chances pour des graines d'arbres de devenir des semis ont été faibles, l'établissement des semis était relativement élevé pour *Picea*, intermédiaire pour *Abies* et *Acer* et faible pour *Fagus*.

La probabilité qu'une plantule soit broutée augmentait avec sa taille et diminuait avec la hauteur des herbacées voisines et la présence de buissons protecteurs. Elle était la même pour les quatre espèces et avec des pressions de broutage faible et élevée. Les plantules ont montré des réponses spécifiques aux espèces et à la taille pour leur survie et leur croissance. Sous une faible et une forte intensité de broutage, les petites plantules de conifères avaient un taux de survie plus faible (36 %) que celles des feuillus (53 %), certainement en relation avec de plus grandes pertes de biomasse liées à une architecture plus vulnérable des plantes. Sous de faibles intensités de broutage, les grandes plantules de *Picea* (80 %) et *Fagus* (67 %) avaient une meilleure survie que celles d'*Acer* (50 %) et *Abies* (33 %). Ceci était probablement dû aux différences dans les tolérances des plantules à la perte de biomasse.

Le dommage résultant de la simulation de broutage a produit de faibles pertes de biomasse lorsque les petites plantules grandissaient lentement en présence des voisins herbacés. L'ombrage a augmenté cet effet. Au moins à court terme, le degré de tolérance des petites plantules n'était pas lié à la santé des plantes (*i.e.* la probabilité de survivre et la croissance) puisque les plantules qui compensaient presque toute leur perte de biomasse avaient encore une santé plus faible que les plantules moins tolérantes. *Picea* fut la seule espèce non négativement affectée par une forte irradiance comme celle que l'on trouve dans les pâturages ouverts.

Pour toutes les espèces d'arbres, la facilitation d'un buisson protecteur sur une plantule a été la plus grande à une intensité moyenne de broutage. Les buissons étaient plus fortement endommagés à forte qu'à faible intensité de broutage. En conséquence, la probabilité d'échapper au broutage, de survivre ou de grandir augmentait lorsque la plantule sous le buisson était soumise à une faible mais pas à une forte intensité de broutage. De plus, les effets positifs des buissons tendaient à être plus élevés pour les conifères et en particulier pour *Picea* qui était plus sensible à la fois à la compétition par les voisins herbacés et au broutage.

En conclusion, la résistance des arbres à l'activité du bétail varie entre les premiers stades d'établissement des arbres et dépend des essences, des intensités de broutage et des conditions environnementales. Des interactions à la fois compétitives et facilitatives trouvées entre les jeunes arbres et la végétation qui les accompagne illustrent la nature complexe des interactions plantes-plantes et plantes-animaux durant la phase d'établissement des arbres en pâturages boisés. L'aperçu des interactions entre le broutage des plantes par les vaches et l'établissement des arbres en milieux semi-ouverts contribuera à renforcer la théorie et les modèles écologiques, comme à procurer des éléments de gestion et de conservation pour ces écosystèmes.

Mots-clés: broutage, compétition, conservation, dynamique des écosystèmes, facilitation, expériences en champs, écologie du broutage, plantation, piétinement, survie des plantules, émergence des semis, ensemencement, montagnes du Jura suisse, diversité des arbres, établissement des arbres, espèces d'arbres, résistance, système sylvo-pastoral, tolérance.

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Chapter 1

Introduction

1.1 Wood-pastures

Wood-pastures are semi-natural, high biodiverse ecosystems, which are found in places with a very long history of extensively livestock grazing and forest management (Gillet and Gallandat 1996a). Large herbivores drive the vegetation dynamics of wood-pastures through the maintenance of mosaics of grassland, shrub thickets and woodland patches (Olff *et al.* 1999; Gillet *et al.* 2002; Bakker *et al.* 2004; Smit *et al.* 2006). Within the context of nature conservation, successful management is severely hindered by the lack of ecological knowledge about the effects of large herbivores on woody species (Bokdam and Gleichman 2000).

The formation and maintenance of wood-pastures is explained by a theory called *'the cyclic turnover of vegetation'* (Vera 2000). Unpalatable or thorny plants and shrubs, invading open grasslands, facilitate tree establishment since they protect young trees from being browsed (Smit *et al.* 2006). In this way, trees advance into the grassland at the same place as the spreading fringes of the thorny, unpalatable nurse plants. As trees will grow, they will outcompete in turn the plants that facilitated them, leading to the creation of woodland. Regeneration of trees inside the woodland is limited due to browsing and trampling by large ungulates present in wood-pastures (Bakker *et al.* 2004). When mature trees die, open areas in the woodland are formed. Establishment of trees in these open areas will still be prevented by the large herbivores. Grasses, whose seeds are often brought in by large herbivores, establish themselves and grassland patches are formed and maintained by grazers. Once grassland patches are sufficiently large enough and grazing pressure not too high, young trees can emerge again from the grassland via protection by shrubs (Olff *et al.* 1999; Vera *et al.* 2006). When this cyclic succession becomes spatially asynchronized, it will result in shifting mosaics of grassland, shrub thickets and woodland patches (Olff *et al.* 1999; Vera 2000; Gillet *et al.* 2002).

The above-described process shows that large herbivores are necessary to maintain the changing balance between plant competition and facilitation processes in wood-pastures. However, large herbivore pressure may be too high (intensification), preventing shrubs or trees to regenerate, or too low (extensification), preventing grassland to regenerate due to tree encroachement. In case of departure of the equilibrium between extensification and intensification, wood-pastures will evolve towards either closed forests or open pastures with concomitant loss of biodiversity (Figure 1.1). Recently, Vera (2000) speculated that the former (8000-5000 BP) lowland temperate zone of Europe existed out of wood-pastures, driven by (extinct) wild, large herbivorous (*e.g.* aurochs, tarpan, bison) preventing the dominance of closed canopy forests. His theory is in contrast with the widely accepted theory that Europe was dominated by high, closed-canopy, mixed-deciduous primeval forests before the onset of human impact. Although Vera's idea and the origin of wood-pastures is currently questioned (Birks 2005; Mitchell 2005; Moore 2005), no doubts exist about their high cultural, socio-economic, ecological and landscape value.

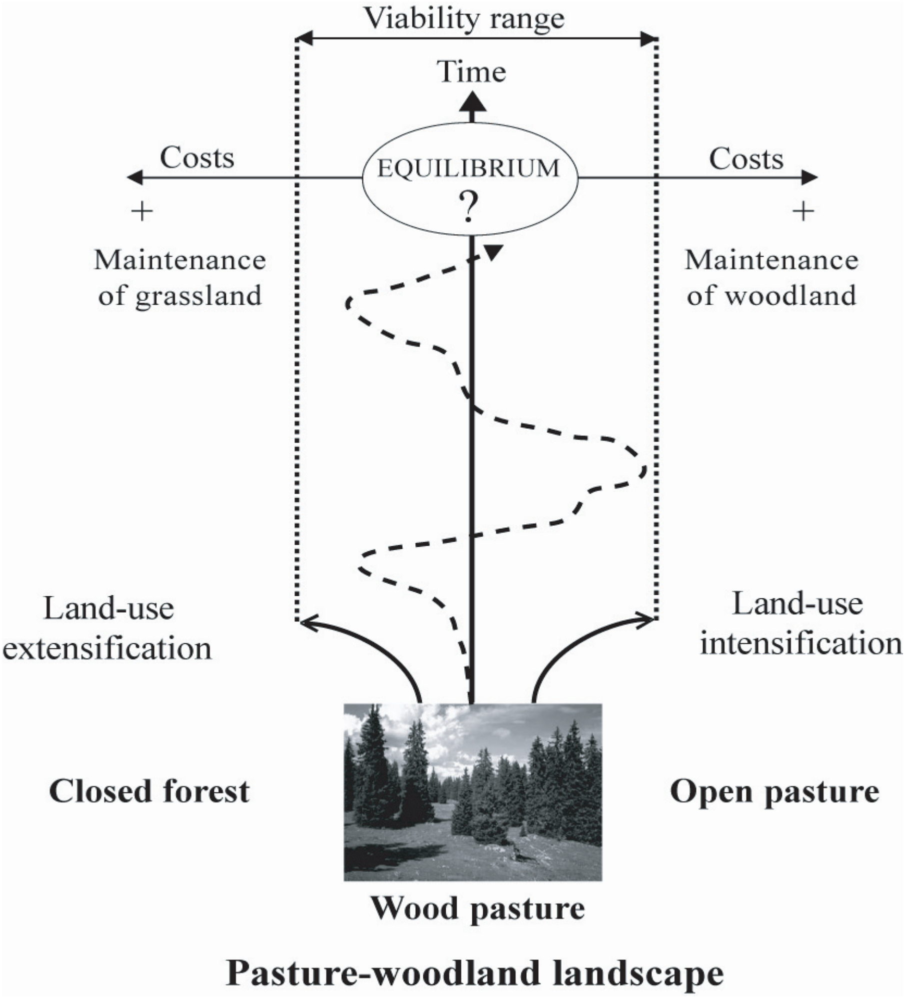

Figure 1.1 Wood-pasture landscape dynamics as a result of unstable equilibrium between extensification and intensification (adapted and translated from Combe 2001).

Current changes in agricultural practices are leading to either intensification or abandonment and as a result most of the ancient wood-pastures in Europe suffered a dramatic decline during the last century (Gillet and Gallandat 1996 b; Rackham 1998; Vera *et al*. 2006). Several examples of ancient wood-pasture in temperate Europe remain, for example in the Swiss Jura Mountains. Within the context of nature conservation, there is an increasing need to develop conservation tools. Consequently, during recent decades, several nature development projects in Western Europe used the (re-) introduction of large domesticated or wild herbivores to induce and increase community diversity by creating habitat heterogeneity (Van Wieren *et al.* 1997; Olff and Ritchie 1998; Gordon *et al.* 2004; Rook *et al.* 2004; Danell *et al*. 2006). Moreover, not only in Europe but worldwide there is a growing interest in combining silviculture and agriculture to develop silvopastoral systems which are both biodiverse and socio-economically viable (Etienne 1996; Hobbs and Yates 2000; Teklehaimanot *et al.* 2002; Lehmkuhler *et al.* 2003; Asner *et al.* 2004; Kirby 2004). In silvopastoral ecosystems, the question of management type and use of intensity is critical. Successful management requires scientific observation and experimentation but was untill recently especially based on anecdotal evidence (but see Bakker *et al*. 2004; Kohler 2004; Smit 2005). The understanding of the main ecological processes occurring in wood-pastures is essential for efficient management schemes of this threatened ecosystem.

1.2 Tree regeneration: from seed to sapling

Trees are classified as tall species, with long-living woody stems and perennating buds emerging from aerial parts. At maturity, they have secondary branches supported on a single main stem or trunk with apical dominance (Bernatzky 1978). Trees gain dominance in many vegetation communities because of their size, longevity and ability to survive under stressful conditions like low light conditions, drought and fire (Grime 1979). Though, it takes a long and difficult pathway to achieve dominance and a tree meets the hazards of each layer of vegetation that it penetrates during its regeneration process. Especially in the lower vegetation layers, during the early stages of establishment, trees are affected by a great range of biotic and abiotic factors. Consequently, the establishment phase of trees can be considered as more vulnerable to environmental constraints than the adult phase (Harper 1977; DeSteven 1991a, 1991b; Smit 2002; Lloret *et al.* 2005).

The early phase in the life cycle of a tree exists out of different sequential stages:

- seed stage
- seedling stage (< 1 year)
- sapling stage (1 – 8 years)

Each stage has to cope with several hazards. Most trees depend on wind or animals to disperse their seeds and to reach new sites. Seeds are for example vulnerable to desiccation and predation by fungal, insectivorous and mammalian predators (Fenner 1985; Farmer 1997). After germination, which is complete as soon as the radicle ruptured the seed coat, a number of environmental factors may impede tree seedling and sapling establishment in pastures such as: soil compaction, lack of soil nutrients, competition from neighbours, seasonal drought, limited light availability, excessive irradiance, high temperature and predation (Gill and Marks 1991; Farmer 1997; Holl 1999; Myster 2004).

1.3 Cattle grazing and tree regeneration

1.3.1 Cattle diet

The diet of large herbivores can be distinguished by the degree to which they contain browse (*i.e.* woody species) or grasses (Hofmann 1989; Gordon 2003). Animals which consume mainly browse and are committed to woodland for habitat use are true browsers (*e.g.* moose (*Alces alces*) and roe deer (*Capreolus capreolus*)). Herbivores which specialize on a grass diet and concentrate most of their feeding outside woodland or in open areas of a savannah-like landscape are grazers (*e.g.* cattle (*Bovis* spp.), horses (*Equus* spp.) and sheep (*Ovis* spp.)). Those which feed on a mixture of both plant types are mixed or intermediate feeders (*e.g.* chamois (*Rupicapra rupicapra*) and red deer (*Cervus elaphus*)).

Cattle generally avoid most woody species due to high levels of difficult-to-digest lignin and secondary metabolites, and select for a grass-based diet with a high digestibility and high N and P contents (Gordon 2003; Mayer *et al.* 2003). However, by feeding on seedlings and saplings opportunistically, cattle has been identified as an important factor regulating tree regeneration in wood-pastures (*e.g.* Lehmkuhler *et al.* 2003; Bakker *et al.* 2004; Mayer *et al.* 2005; Smit *et al.* 2006). The effects of large (domesticated) grazers on herbaceous plant communities were frequently investigated in grassland systems (WallisDeVries *et al.* 1998; Bakker 2003; Gordon 2003; Kohler 2004; Rook *et al.* 2004) but their effects on tree establishment in the herbaceous layer received however little investigation, and was mainly carried out in (semi-) arid systems such as savannas (Archer *et al.* 2001; Tobler *et al.* 2003; Asner 2004).

1.3.2 Direct effects of cattle on tree regeneration

Cattle can directly affect early tree establishment via browsing (biomass off-take) and trampling (Lewis 1980; Fritz *et al.* 1996; Dockrill *et al.* 2004; Griscom *et al.* 2005). In general, browsing and trampling will reduce seedling and sapling growth rates and/or survival chances. Consequently, a cattle foraging behaviour decision of a few seconds might have an impact during decades on the tree pattern. The impact of browsing is dependant on the severity or repetition of damage and herbivore densities (Bergström and Danell 1987; Brooker *et al.* 2006), but also on the plant itself and the (biotic and abiotic) environmental conditions in which the tree is growing.

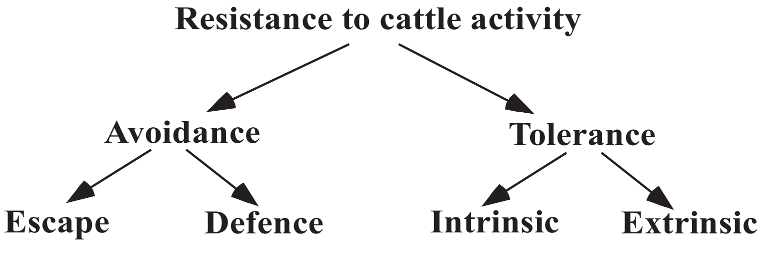

Figure 1.2 Avoidance and tolerance are two resistance mechanisms that trees express to reduce negative impacts of their interactions with cattle (derived and adapted from Boege and Marquis 2005; Hester *et al.* 2006).

Tree resistance to cattle activity consists out of two mechanisms: avoidance (escape and defence) and tolerance (Fig. 1.2; after Boege and Marquis 2005; Hester *et al.* 2006). Escape includes traits that reduce the likelihood of being found by grazers such as location, size and visibility (or apparency). Defence includes traits that reduce plant quality as food for browsers such as secondary metabolites, thorns and spines. Tolerance includes traits that reduce the negative grazing and non-grazing impacts (*e.g.* trampling) of large herbivores on plant fitness. Tolerance comprises the ability of the tree species to persist with reduced biomass and to compensate for biomass loss through active regrowth relatively to ungrazed plants and depends on two factors: 1) intrinsic factors which are determined genetically or developmentally (*e.g.* protected meristems, branching responses, distribution of buds, growth plasticity) and 2) extrinsic factors such as environmental available resources for growth. Extrinsic factors influencing plant tolerance are normally those which may allow increased plant growth, nutrient uptake and light acquisition following browsing damage. It is generally accepted that a plant's tolerance of grazing is greater in low-stress, resource-rich environments (Belsky 1986; Maschinski and Whitam 1989). For example, a sapling will be more tolerant under light conditions than shaded conditions (McLaren 1996). However, this relationship is not always supported by empirical results and a higher tolerance under high-stress, low-resource rich environments was found (Hawkes and Sullivan 2001; Puettemann and Saunders 2001; Wise and Abraham 2005). Stressed plants may for example be more attractive to herbivores due to lower concentrations of defensive chemicals (White 1993).

Different tree species likely have different resistance towards cattle activity due to differences in architecture, chemical composition and resource allocation (Grime 1979; Gill 1992). Moreover, owing to resource allocation and architectural constraints in trees, and the influence of herbivore foraging behaviour, resistance to herbivores is likely to change during tree development. Tolerance to herbivore damage appears to be low for small tree seedlings if cotyledons are lost. As young trees grow and the shoots become thicker and more lignified, digestibility declines and mainly distal parts are likely to be browsed. So, younger and smaller trees are generally more susceptible than larger and older trees (Boege and Marquis 2005; Gill 2006).

The protection of saplings by unpalatable or thorny plants, *i.e.* associational resistance, is an important process driving wood-pasture dynamics (Smit 2005). When the main stem of a tree grows out of reach of cattle (*i.e.* about 1.50 m), the tree will be able to grow without constraint (Vila *et al.* 2003). To reach this size, trees may need however more than one hundred years due to frequent browsing episodes (Gallandat *et al.* 1995).

1.3.3 Indirect effects of cattle on tree regeneration

The success of tree regeneration can be strongly influenced by either competitive or facilitative interactions with neighboring plants (Kareiva and Bertness 1997; Myster 2004; del-Val and Crawley 2005) and large herbivores can affect regeneration indirectly by altering the relative strength of these effects. Generally, grasses reduce sites for germination, and limit growth and survival rates of established saplings (Gill and Marks 1991; Davis *et al*. 1999). Competition for light, water, nutrients and space can however be reduced by cattle activity through decreasing herbaceous biomass via grazing and gap creation via hoof pressure (Karl and Doescher 1993; Posada *et al.* 2000; Van Auken 2000). Due to reduced competition, grazing might also contribute to shrub encroachment in grasslands, as found in (semi-) arid regions (Westoby *et al*. 1989; Van Auken 2000), which might facilitate on their turn sapling establishment through protection against large grazers (Smit *et al*. 2006). Furthermore, cattle can indirectly increase tree establishment by reducing seed and seedling predator abundances (Goheen *et al.* 2004; Smit *et al.* 2001) or decrease establishment via soil compaction limiting root penetration (Rawlinson *et al.* 2004). Via defecation, urination and selective foraging, large herbivores can increase or decrease soil nutrient availability, depending on environment and herbivore densities (Pastor *et al*. 2006).

1.4 Thesis project

1.4.1 Aims and outline

The main objective of this study is to investigate the impact of cattle activity on the early stages of tree establishment for four tree species common in the wood-pastures of the Swiss Jura Mountains. Cattle can have both direct and indirect effects on tree establishment and the interaction between cattle activity and both competition and facilitation by surrounding vegetation is studied. It is evaluated how detrimental effects of different cattle grazing intensities contribute to overall tree seedling or sapling survival and growth. Results are based on experimental field studies and empirical evidence is provided.

Five different field studies are presented as individual chapters in this thesis. In all studies, the four tree species (see below) are used as target species. In chapter **two**, I present an experiment on the effects of openings in the herbaceous layer on tree seedling establishment during the first three months after seed sowing. Gaps can be a result of indirect cattle activity namely trampling. The effects of gap size on seedling emergence, growth and survival are investigated for each of the four tree species. In chapter **three**, the results of a second seed sowing experiment are presented. This experiment combines the effects of openings in the herbaceous layer and cattle grazing disturbance on tree seedling establishment during the first year after sowing. In chapter **four**, a transplantation experiment tests for the effect of cattle on browsing frequency and growth of different-sized saplings. Saplings were transplanted under zero, low and high grazing intensities and their fate was followed for three months. In chapter **five**, a simulated browsing experiment tests for tolerance of transplanted saplings under controlled environmental factors competition from neighbours and shading. Compensatory growth and survival responses for each of the four tree species were followed during two growing seasons. In chapter **six**, the role of facilitation for tree regeneration in wood-pastures was investigated. Inter-specific browsing frequency, survival and growth responses with and without protection from a nurse shrub along a grazing intensity gradient were monitored during one year. In chapter **seven**, I summarise and combine the findings of the different studies in order to come to a synthesis of the importance of cattle activity on early tree establishment in wood-pastures. The experimental design of each field study (Chapters 2 - 6) is presented in the appendices.

1.4.2 Tree species

The selected target tree species co-occur in the wood-pastures of the Swiss Jura Mountains between an altitude of 800 and 1.200 m a.s.l. The target tree species have different growth strategies making them interesting species for a comparative study involving browsing resistance from both scientific research and management perspective.

I separate the species, which are all native to Europe, in two groups (based on Grime 1979; Gill 1992; Young and Young 1992; White 1995; Pagès *et al*. 2003; White *et al.* 2005):

Coniferous, evergreen species

Coniferous species are supposed to have a low tolerance to herbivore damage and biomass losses due to low flexible growth patterns and stored reserves (carbohydrates and nutrients) in needles. They might however be avoided by cattle due to low palatability and tough needle-like leaves.

→ *Abies alba* L. (Fam. Pinaceae)

Silver fir is a common, shade-tolerant forest tree in cool northern or mountain forests of mainland Europe. The seed (8-15 mm long) has a large wing (10-15 mm), brownish coat and is wind dispersed.

→ *Picea abies* L. Karst (Fam. Pinaceae)

Norway spruce is a common, moderate shade-tolerant and widespread tree covering central and northern Europe, Scandinavia, north-west Russia and several European mountain regions. The seeds are 4-5 mm long, with a pale brown 15 mm wing and depend on wind for dispersal. *Picea abies* is currently dominant in many wood-pastures of the Swiss Jura Mountains (Gallandat *et al*. 1995), partly due to timber management, but cattle grazing is thought to play a role on the current tree species pattern.

Broad-leaf, deciduous species

Deciduous species are supposed to be more tolerant to herbivore damage than coniferous species since reserves are mainly stored in stem and roots resulting in a greater ability for compensatory growth. However, they may be less avoided by cattle due to higher leaf nitrogen content.

→ *Acer pseudoplatanus* L. (Fam. Aceraceae)

Sycamore maple is a fast-growing, moderate-shade tolerant, pioneer tree and native to central Europe from France to Poland, south (in mountains) to northern Spain and Turkey. Each seed (5-10 mm in diameter) has a 20-40 mm long wing with modest potential for wind-dispersal.

→ *Fagus sylvatica* L. (Fam. Fagaceae)

European beech is a fast-growing, shade-tolerant forest tree, natural ranging from southern Sweden to central Italy, France, northern Portugal, and east to northwest Turkey. The seed is a small triangular nut, 15-20 mm long and animal dispersed.

1.4.3 Study sites

In the Swiss Jura Mountains, wood-pastures occur in the mountain and subalpine belts, mainly at an elevation between 800 m and 1400 m a.s.l. (Gillet and Gallandat 1996b). The climate of this area is predominantly oceanic with a mean annual rainfall of about 1600 mm at 1200 m a.s.l. (with more than 400 mm snow precipitation) and a mean annual temperature of 7 °C. At 1200 m a.s.l., mean day temperature is below 0 °C on more than 60 days per year and the ground is generally covered with snow from December to April.

The studies of this thesis were performed in two different sites located in the central part of the Swiss Jura Mountains (Fig. 1.3): La Petite Ronde (Chapter 2, 3, 4 and 6; Appendix 1) and La Frétaz (Chapter 5, Appendix 5). Both sites are rented and managed by the agronomic research stations Agroscope Changins-Wädenswil ACW (Switzerland). Like in other temperate mountainous regions, the climate limits cattle management to the summer period, from the end of May to the end of September. A 'rotational-grazing' system is accorded to the pastures which are subdivided into paddocks. Cattle herds (mainly heifers) circulate from one paddock to another according to a variable number of grazing rotation periods (between 3 and 5 rotations per season, corresponding to a stay in each paddock of 10 to 30 days). 'Free ranging' systems (the animals spend the whole summer season roaming freely through the pastures) can still be found elsewhere but more and more wood-pastures are now managed according to the rotational grazing system, with the aim of optimizing the utilization of the resources. In both sites, all naturally established saplings died due to high cattle grazing intensities or were mechanically removed by the farmers. Naturally occurring large herbivores in our sites are roe deer (*Capreolus capreolus*), chamois (*Rupicapra rupicapra*), wild boar (*Sus scrofa*) and mountain hare (*Lepus timidus*).

Figure 1.3 Location of the study sites "La Petite Ronde" and "La Frétaz" in the Swiss Jura Mountains (Switerland).

Chapter 2

Competitive effects of herbaceous vegetation on tree seedling emergence, growth and survival: does gap size matter?

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Abstract

Question: What is the effect of gap size on the seedling emergence, growth and survival of 4 common tree species in wood-pastures?

Location: A pasture in the Jura Mountains, Switzerland.

Methods: Seeds were sown in a complete three-way factorial design with eight blocks in May 2003. Each block consisted of a competition treatment (4 gap sizes including zero) and a mowing treatment (mown and unmown). Emergence, survival and total biomass of tree seedlings of three species (*Picea abies, Acer pseudoplatanus* and *Fagus sylvatica*) were measured. A fourth species (*Abies alba*) failed to germinate.

Results: Gaps had a positive influence on the early stages of tree development for all species. Larger gaps favoured growth and survival more than small gaps. Seedling growth was higher when vegetation around the openings was mown. Mowing the vegetation at gap size zero enhanced both growth and survival compared to unmown vegetation. Mown gaps larger than zero had increased seedling desiccation but decreased seedling predation. Species showed similar trends in their emergence and growth responses to gap size and mowing treatments but for *Picea* emergence rate was higher and survivorship was lower than for *Acer* and *Fagus*.

Conclusions: Gap size does matter for tree seedling success but even in more favourable large gaps only a small percentage of seedlings emerged and survived. The effects of gaps on tree seedling establishment are complex as a result of interactions between biotic and abiotic changes caused by gaps.

Keywords: competition, opening, sowing experiment, trampling, tree establishment, wood-pastures

2.1 Introduction

Gaps are openings in swards which allow partial release from competition and provide opportunities for establishment of plants from seed (Aguilera and Lauenroth 1995; Bullock *et al.* 1995; Kotanen 2004) which may be particularly important for woody plants (Mazia *et al.* 2001; Jurena and Archer 2003; Rousset and Lepart 2003). They may be created by local disturbances such as frost heave or plant death but they are most often created by animal activity, such as digging (Goldberg and Gross 1988; Kotanen 1995) and trampling (Trimble and Mendel 1995). In wood-pastures, where a mosaic of grasses, shrubs and trees is maintained by grazing (Olff *et al.* 1999), tree establishment is necessary for the continued existence of the system. Tree seeds will often experience competition from herbaceous vegetation during seedling establishment, so gaps may be essential for the persistence of these systems.

Since plants compete for light, water, nutrients and space, gaps are expected to have positive effects on tree seedling emergence (Nilsson *et al.* 2002), survival and growth (Prach *et al.* 1996; Davis *et al.* 1999; Meiners and Handel 2000). A reduction in height of the surrounding vegetation, for example caused by grazing, may also reduce competition and create enhanced conditions for tree seedlings to establish (Karl and Doescher 1993). However, under dry weather conditions, the moist microclimatic conditions within the sward may be more favourable than exposed soil. Therefore, gaps may also have negative or neutral effects on tree seedling emergence (Burton and Bazzaz 1991; DeSteven 1991a; Gill and Marks 1991) and survival (Berkowitz *et al.* 1995).

The physical and biological environments within gaps vary with gap size (Pickett and White 1985). In cattle-grazed semiarid grasslands, gaps caused by disturbance are commonly 30-50 cm across (Hook *et al.* 1994). Larger gaps have greater light availability and are generally drier and warmer due to enhanced evaporation, and seedlings will experience less root competition for soil water and nutrients (Hook *et al.* 1994). An influence of gap size on emergence, growth and survival in newly created gaps has been found for herbaceous species (McConnaughay and Bazzaz 1987; Bullock *et al.* 1995; Kotanen 1997) and for light-demanding trees in forests (Platt and Strong 1989). Furthermore, the positive effects of openings, such as increasing light availability may decrease with time due to overgrowth. In contrast, progressive shading of the gaps by surrounding vegetation will cause a reduction in evaporation and provide protection against heat injury, often responsible for high seedling mortality (Farmer 1997). To our knowledge, no information about the influence of gap size in grassy swards on the emergence and subsequent growth and survival of tree seedlings is available.

An understanding of the ability of trees to regenerate in wood-pastures of the Swiss Jura Mountains is needed for the preservation of these biodiverse systems in the face of changing agricultural patterns. The ability of different species of tree seedlings to compete with herbs and grasses can be expected to vary due to their variable light requirements, growth strategies (Young and Young 1992; Brzeziecki and Kienast 1994) and seed sizes (Seiwa and

Kikuzawa 1996). Therefore, the objective of our study was to investigate the effect of gap size on seedling emergence, growth and survival of each of four tree species. We hypothesized that (i) gaps have a positive effect on seedling emergence, survival and growth due to a reduction in competition, (ii) seedling emergence, growth and survival vary among gap sizes due to a different microclimate and (v) the four tree species differ in their ability to emerge, grow and survive in competitive conditions.

2.2 Methods & Materials

2.2.1 Study site

A traditionally managed grazed pasture in the Swiss Jura Mountains (la Petite Ronde, 6°27'26" E, 46°56'22"N, altitude 1125 m a.s.l.) was selected. The vegetation, dominated by *Festuca rubra* and *Agrostis capillaris*, belongs to the fertilized pasture of low and mid altitude of the *Cynosurion*. The pasture is surrounded by a beech-fir forest of the *Abieti-Fagenion* (Delarze *et al.* 1998). It has been grazed in spring and summer by cattle for centuries under a rotational grazing system. The growing season of 2003 was particularly hot and dry (Table 2.1).

We used the four most common local tree species as targets: the evergreen *Picea abies* and *Abies alba* and the deciduous *Acer pseudoplatanus* and *Fagus sylvatica*. We bought seeds harvested from regional montane sites at altitudes similar to that of our field site from a local nursery (Lobsigen, Switzerland). Seeds were cold-stratified (4°C) in wet sand to break seed dormancy, for two (*Fagus*) or eight (*Abies* and *Acer*) weeks (Burkart 2000) until one day before sowing. The wings of the *Acer* seeds were cut off to avoid them being displaced by the wind. *Picea* seeds were humidified in Petri-dishes for 48h before sowing (Young and Young 1992). One hundred (*Picea* and *Abies*) or 50 seeds (*Acer* and *Fagus*) were sown along a 45 cm sowing line in the centre of each gap in mid-May 2003. Seeds sown on bare soil were slightly covered with soil in order to prevent displacement by wind. Seeds sown into intact vegetation were placed on the soil surface without disturbing the roots of the vegetation. Seed germinability was also tested in May using 240 seeds of each species in a greenhouse pot experiment a with randomised design. *Abies* seeds did not germinate, either in the field or in the greenhouse, and this species is dropped from the analysis and is not discussed further.

Table 2.1 Ten-year average (1994-2003) and 2003 annual + monthly (duration of the experiment) mean temperature (°C ± SD) and mean precipitation (mm ± SD) at the field site (Les Verrières, CH).

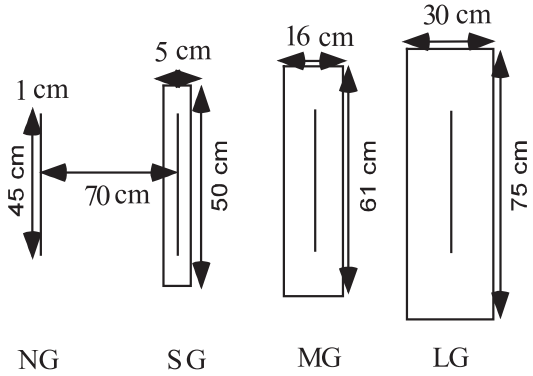
	10-year average		2003	
	°C	mm	°C	mm
Annual	7.4 ± 1.0	1607.0 ± 547.7	7.8 ± 1.0	980.0 ± 42.0
May	9.9 ± 2.2	190.3 ± 69.6	10.1 ± 4.1	151.2 ± 9.1
June	13.0 ± 2.2	124.5 ± 65.9	18.0 ± 2.2	34.6 ± 8.5
July	14.6 ± 1.7	161.8 ± 56.0	16.5 ± 3.9	146.0 ± 9.3
August	15.3 ± 2.0	146.1 ± 45.3	20.0 ± 7.9	108.2 ± 7.9

2.2.2 Experimental design

We used a blocked factorial design with eight blocks and three factors: species, gap size and mowing. Four gap sizes were used: zero (no gap, NG), small (SG), middle (MG) and large (LG) (Fig. 2.1, Appendix 2). To create the gaps, aboveground vegetation was removed and all shoot bases and rhizomes were dug out with a knife. The edges of all gaps, except NG, were trenched to 20 cm to reduce belowground competition by neighbouring roots. The mowing treatment had two levels: mown and unmown. The vegetation of NG and around the openings of the mowing treatment was mown bimonthly to a height of 5 cm and the openings were hand-weeded every two weeks.

Two exclosures of 38 m x 15 m and separated by 100 m, were constructed in the pasture. Within each exclosure, four blocks (8.5 m x 5.6 m) were laid out at 3 m intervals. Each block was split into two plots and the mowing treatment was randomly assigned. In each plot, treatments were randomly assigned to each of 16 subplots (*i.e.* 4 gap treatments x 4 tree species) separated by at least 70 cm (measured sowing line to sowing line, Fig. 2.1), resulting in a total of 256 experimental units.

Figure 2.1 Experimental design. Subplot measurements. Seeds were sown along a 45 cm line. Sowing line of SG (small gap), MG (middle gap) and LG (large gap) was made 1 cm deep. NG (no gap) represents intact vegetation.



2.2.3 Data collection

Seven times during the growing season (04/06, 13/06, 19/06, 29/06, 18/07, 16/08, 22/08), we recorded the number of new seedlings that had appeared and the number of dead (or missing) seedlings. A seedling was noted as emerged if it had developed its cotyledons. Individuals were marked by placing coloured tooth-picks next to the seedling, using a different colour for each observation period. The fate of each emerged individual was monitored. The cause of death was noted as: 1) desiccation (seedling intact but dry), 2) predation (observable damage due to insects, slugs or voles or, when seedling was missing, presence of vole faeces or mounds) or 3) missing (seedling not found). *Picea* seedlings were difficult to detect in the tall vegetation of the unmown NG treatment and were not counted until the last observation, therefore no emergence or survival data are available for these 8 subplots. All live seedlings were harvested on 22 August 2003 and separated into leaf, stem and root sections. Each subcomponent was oven-dried and weighed.

Light penetration (% above-canopy sunlight reaching the soil surface) was measured for each plot in July (for NG the sensor was placed within the herbaceous layer) using a 40 cm light probe (Decagon Sunfleck Ceptometer, Delta-T Devices LTD, Pullmann, WA, USA).

2.2.4 Data analyses

All statistical analyses were done with R, version 2.0.0 (R Foundation for Statistical Computing, 2004).

Because there were no significant differences in germination percentage among species in the greenhouse trial (germination percentage ± 1 SE *Picea* 55 ± 4.1 %, *Acer* 52 ± 4.0 %, *Fagus* 57 ± 7.2 %; one-way anova, F = 1.03, d.f. 2, *P* = 0.46), no correction was made for germination rates in the field.

Emergence: A linear mixed-effects model (LME) with restricted maximum likelihood estimation (REML, Pinheiro and Bates 2000) was fitted to investigate the effect of species and gap size on seedling emergence with block included as a random factor. All seedlings emerged during the first month, when vegetation was short. We therefore excluded the effect of mowing from this analysis. The response variable "percentage of emerged seedlings" (sum over season) was arcsine transformed to reduce heteroscedasticity. Because the interaction between species and gap size was found to be significant, we analyzed each species separately. We have chosen SG as a reference level for significance tests because we were particularly interested in comparing this gap size with others.

Growth: To investigate the effect of gap size and mowing on total seedling biomass, a LME model was fitted as described above. Seedling biomass (g) was log transformed to reduce heteroscedasticity and LG was chosen as reference level. Comparisons of seedling biomass among species are not meaningful. In addition, a LME model was fitted to measurements of the root:shoot ratio, after log transformation, to estimate the effect of mowing. Total biomass was included in the model as a covariate.

Survival: The effects of species, gap size and mowing on seedling survival (binary data) were investigated. Again, significant interactions between species, gap size and mowing were found, and we separated the analysis by species. To model a binary response to categorical treatments, we fitted a generalized linear model (GLM) with a binomial distribution and logit link function (Venables and Ripley 2002). Because block effects are difficult to interpret in a model with categorical data, we simplified the model to include, 'exclosure' (two levels, see above) as the first explanatory variable. The number of observations for the NG treatment was low, which caused large variances, but a re-analysis excluding this gap size produced similar results.

The influence of species and mowing treatment on the cause of death were analyzed with a 3-way contingency table. Testing was carried out by using the difference in deviance between the models (GLM with number of dead saplings as response, three categorical factors, their interactions, Poisson distribution and log link function) with and without the corresponding interaction using “drop” function in R (Venables and Ripley 2002). Because the seedlings were not strictly independent experimental units, the results of this analysis should be viewed as indicative rather than definitive.

2.3 Results

2.3.1 Seedling emergence

A significant interaction between gap size and species was found (Table 2.2). Emergence rates for *Picea* were higher for all gap sizes (mean: 24 %) than for *Acer* (11 %) or *Fagus* (14 %) (Fig. 2.2), but the magnitude of the difference varied with gap size. In 11 *Acer* and 10 *Fagus* subplots no seedlings at all emerged. All species emerged significantly better in openings than in NG. MG and LG did not differ significantly from SG, nor were there consistent trends (Fig. 2.2).

Table 2.2 Effects of gap size, species and their interaction on seedling emergence and effect of gap size per species on emergence (LME). Mowing treatment is not included in the analysis.

	All	*n*=184		*Picea*	*n*=56		*Acer*	*n*=64		*Fagus*	n=64	
	df	F		df	F		df	F		df	F	
Gapsize	3	23.01	****	3	2.466	ms	3	4.135	*	3	28.05	****
Species	2	29.45	****									
GxSp	6	2.344	*									

P < .05*; *P* < .01**; *P* < .001***; *P* < .0001****; ms: .05 < *P* < .1

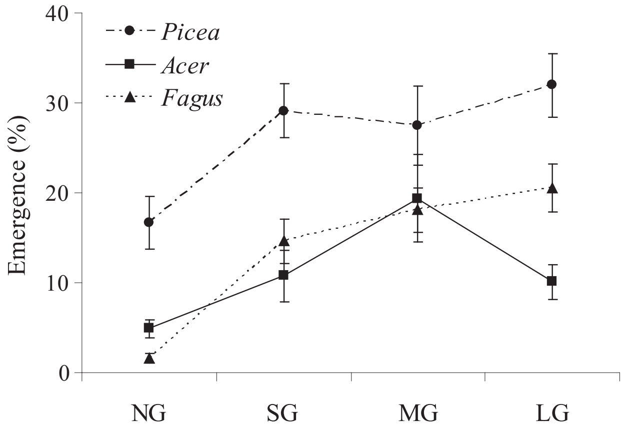


Figure 2.2 Effects of species and gap size on seedling emergence (%) (± 1 SE) in both mown and unmown plots (data taken together). Gap size codes are as in Fig. 2.1.

2.3.2 Seedling growth

Interactions between gap size and mowing were not significant for any species (Table 2.3). Seedling biomass increased both with gap size and with mowing (Fig. 2.3). After controlling for total biomass, we found a significant increase in seedling root:shoot ratio in mown plots for *Acer* (F = 11.7, d.f. = 1, $P < .0001$) and *Fagus* (F = 23.5, d.f. = 1, $P < .0001$) but not for *Picea* (F = 1.8, d.f. = 1, $P = 0.08$).

Table 2.3 Effect of gap size, mowing and their interaction on seedling biomass (LME, analysis per species).

	Picea	*n*=113		*Acer*	*n*=209		*Fagus*	*n*=191	
	df	F		df	F		df	F	
Gapsize	3	55.29	****	3	12.04	****	3	10.47	****
Mowing	1	17.45	***	1	10.96	**	1	5.558	*
GxM	3	2.360	ms	3	0.370	ns	3	1.157	ns

$P < .05$*; $P < .01$**; $P < .001$***; $P < .0001$****; ms: $.05 < P < .1$; ns: non significant result.

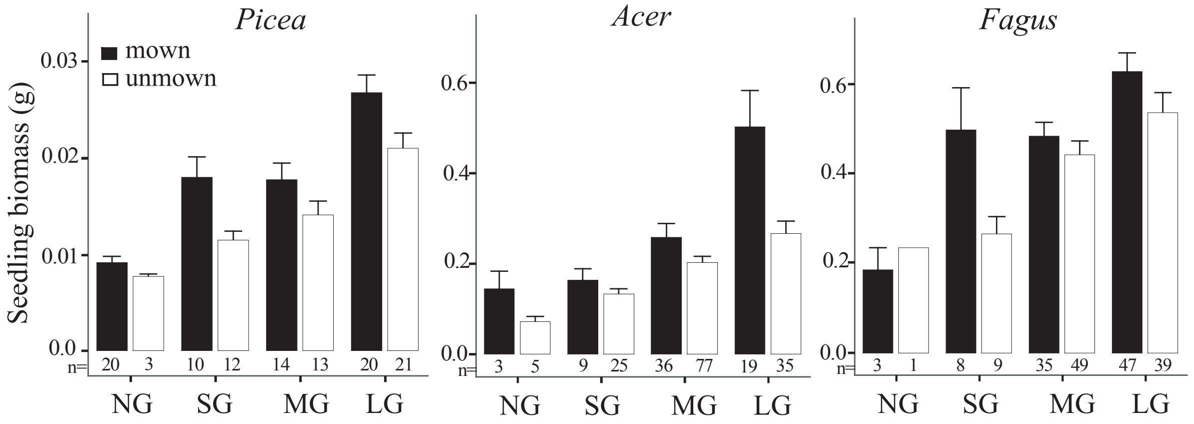


Figure 2.3 Effects of gap size and mowing on total seedling biomass (g ± 1 SE). Gap size codes are as in Fig. 2.1. Note change of scale for *Picea*.

2.3.3 Seedling survival

A significant interaction between species, gap size and mowing was found (d.f. 5, $P < .0001$), so we report the results for each species separately. Overall, 27 % of the *Picea* seedlings, 64 % of the *Acer* seedlings and 44 % of the *Fagus* seedlings survived (Fig. 2.4).

Analysis by species: (i) For *Picea,* the interaction between gap size and mowing was significant (d.f. 3, $P < .0001$). Survival was highest in LG and NG and mowing had a positive effect on survival in LG. In SG and MG, mowing had a negative effect. (ii) For *Acer*, the significant interaction (d.f. 3, $P = 0.01$) seems to be related to a negative effect of mowing in all openings against a positive effect of mowing in NG. Survival was highest in unmown MG and LG. (iii) After deleting an outlier (namely the single surviving seedling out of 8 in NG unmown plots), a marginally significant interaction (d.f. 3, $P = 0.06$) was detected for *Fagus*. Mowing had no effect in the SG, MG or LG, but increased survival in NG, as found for *Acer*. Survival was highest in MG and LG and under mowing treatment in NG.

The most common cause of seedling death was desiccation (Table 2.4). Desiccation was higher in mown plots whereas predation was higher in unmown plots (cause x mowing: $\chi^2 = 170$, d.f. 2, $P < .0001$). *Fagus* seedlings were relatively more predated and more *Acer* seedlings were missing (cause x species: $\chi^2 = 55$, d.f. 4, $P < .0001$).

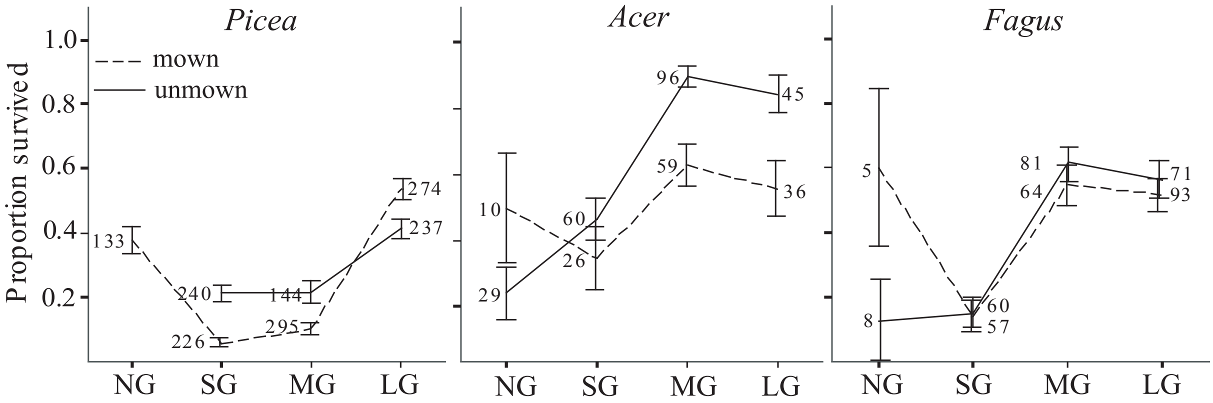
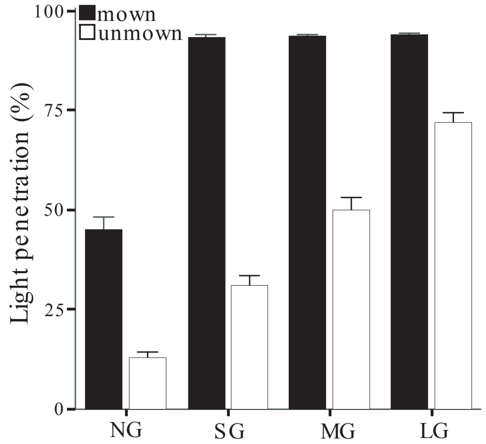


Figure 2.4 Effects of gap size and mowing on proportion (± 1 SE) of seedlings that survived (= number seedlings survived x (number seedlings emerged)$^{-1}$), for each species. Next to each error bar number of observed seedlings is given. Gap size codes are as in Fig. 2.1.

Table 2.4 Percentage of seedlings that died due to desiccation, predation or missing.

		Desiccation	Predation	Missing
Picea	mown	55.5	3.4	0.4
	unmown	28.9	9.9	1.9
Acer	mown	43.6	1.6	0.8
	unmown	28.2	12.9	12.9
Fagus	mown	43.7	7.4	0.0
	unmown	27.3	20.4	1.2

Figure 2.5 Light penetration (%, ± 1 SE) to the soil for each gap and mowing treatment. Results of two-way Anova (response variable was arcsine transformed) for interaction gap size x mowing: F = 26.6, d.f. 3, $P < .0001$. Gap size codes are as in Fig. 2.1.



2.4 Discussion

2.4.1 Seedling emergence

As hypothesized, seedling emergence increased in openings for all species, a result consistent with studies where seedbed scarification and vegetation removal improves tree seedling emergence (*e.g.* Brang 1998; Nilsson *et al.* 2002; Agestam *et al.* 2003). Even under the dry weather conditions of 2003, we did not detect facilitation by herbaceous species, which could be expected due to a moister microenvironment and protection from predators, as has been observed in some old fields (*e.g.* DeSteven 1991a; Burton and Bazzaz 1991). *Acer* and *Fagus* had a very low emergence in intact vegetation, probably because the radicle of seedlings desiccated before penetrating the soil (pers. obs. C.V.). This is a common cause of failure for tree seedlings trying to penetrate the litter layer in forests (Farmer 1997; Caccia and Ballaré 1998). *Picea* emergence may have been more successful because the small seeds could more easily fall into crevices or be buried by shifting soil, and thus obtain greater protection from seed predation and better soil contact for water imbibition. Furthermore, fewer *Picea* seeds may have been eaten by mice than *Fagus* and *Acer* seeds due to their lower energy content (Jennings 1976). Under natural conditions, *Acer* and *Fagus* seeds will fall during autumn and the heavy snow will help them penetrate the litter layer, enhancing the penetration of the root into the soil and thus emergence in spring.

For none of the species were significant differences found between the three sizes of openings. Field observations suggested that the openings were considerably drier than surrounding soil, probably due air flow in trenches between the plot and the surrounding soil, resulting from the method used to create the openings (pers. obs. C.V.). Unusually warm and dry conditions during the growing season of 2003 may have dried the soil of all gaps enough to mask potential differences in emergence between sizes of openings, and our results may be more indicative of patterns to be expected under climate change than past patterns.

2.4.2 Seedling growth

Vegetation removal had a strong positive effect on seedling growth, as has been found by others (Berkowitz *et al.* 1995; Burton and Bazzaz 1995; Nilsson and Örlander 1999). Reduced water, nitrogen and light availability in the herbaceous vegetation often reduces tree seedling growth as found by studies using transplants (Kübner *et al.* 2000; Thevathasan *et al.* 2000; Löf *et al.* 2004).

For all species, seedling biomass increased with increasing gap size and with mowing of the surrounding vegetation, probably due, at least in part, to increasing light availability. Over time, the unmown openings in the sward became revegetated and shaded. The amount of light reaching the soil was reduced more rapidly in the small gaps, because vegetation around the gaps more quickly overgrew the small gaps than the larger ones. In mown plots, light availability in openings of different size was similar (Fig. 2.5), so other factors must have played a role to produce the gap size effect in these plots. There was minimal competition for water and nutrients with root systems of surrounded vegetation since the gaps were trenched. We suggest that the small gaps, which had a smaller soil volume and a large evaporative surface due to a poor connection with surrounding soil (a result of soil shrinkage under the unusual weather conditions), dried out more rapidly than the larger gaps, causing reduced seedling biomass. Intraspecific competition may also have reduced seedling growth more in the small and middle gaps than in the large gaps, as has been found for *Picea* (Li and Wilson 1998).

The higher root:shoot ratio in mown plots of *Acer* and *Fagus* may reflect a decreased stem allocation due to decreasing light competition, and/or increasing root allocation due to water limitation in the mown plots. Madsen (1994) found that at low levels of soil water content, both growth and root:shoot ratio of *Fagus* seedlings increased with increased light. Water and nutrient stress tend to increase allocation of biomass to the roots and increase length of the tap-root (Nambiar and Sands 1993; Meiners and Handel 2000). Our study may have been too short to observe effects on the allocation pattern of the small *Picea* seedlings, although the root:shoot ratio of one-year old *Pinus* saplings were found to be relatively stable even under severe water deficits (Watt *et al*. 2003).

2.4.3 Seedling survival

In general, survival tended to increase with gap size. Variations among species may be caused in part by a relatively larger importance of surface humidity for *Picea* seedling survival, since these seedlings are smaller and more shallow-rooted than the two deciduous species. This greater sensitivity may explain the overall higher mortality rate for *Picea* in the dry conditions of 2003.

Relative survivorship was higher in the intact vegetation than we expected. We suspect that established seedlings in the intact vegetation were less exposed to direct solar radiation and better protected from heat and drought than in openings. Berkowitz *et al.* (1995) proposed similar mechanisms for the facilitation of survival of maple seedlings. In addition, a reduced transpirational surface of the sward, due to grazing or mowing, may have led to increased soil water availability (*cf.* Karl and Doescher 1993).

For all species, seedlings in large gaps had a higher survival rate than in small gaps. As we suggested for the effects on growth, desiccation risk and intraspecific competition may have been higher in small gaps. Increased dryness and higher soil surface temperature in the mown plots probably also caused higher seedling mortality than in unmown plots. The lack of a mowing effect for *Fagus* may have been because higher predation rates in the unmown plots balanced the increased dessication rates in mown plots. The main predators at our study were rodents, but slugs and insects also predated some seedlings (*cf.* Agestam *et al.* 2003). Seedling predation for all species was higher in unmown plots, probably because these plots provided a safer and more attractive environment for rodents and slugs. Gill and Marks (1991) and Ostfeld and Canham (1993) demonstrated that intact vegetation can have an indirect effect on seedling survival by providing a protective habitat for small mammal herbivores that are voracious consumers of newly emerged tree seedlings.

2.4.4 Conclusions and ecological implications

The influence of gaps on tree-grass dynamics are of concern in many grazed ecosystems such as wood-pastures and savannas (Archer 1995; Scanlan 2002). We found that gaps have a positive influence on early stages of tree development. In addition, size- and mowing-related differences in the characteristics of the physical (light, moisture and temperature) and biological (herbaceous vegetation, predators) environment of gaps interacted to influence tree seedling emergence, growth and survival. Although we found larger gaps to favour tree seedling growth and survival, fewer than 20 % of the seeds emerged and survived for three months in favourable large gaps. The dry weather conditions of 2003 were likely not favourable for early tree establishment and this leads us to speculate that increased frequency of such conditions under climate change may need to be taken into account when managing tree pastures.

Compared to our artificial gaps, emerged seedlings in natural gaps will have greater competition for belowground resources because natural gaps are not trenched. Competition for soil water and other belowground resources is then higher in smaller gaps, improving the probability of establishment in large gaps. Further study is needed to understand the balance of above- and below-ground effects under different weather conditions. The duration of moist conditions at the surface may be a critical constraint for tree seedling establishment. Since the characteristics of an opening will depend on the method of its formation and weather conditions, different results in tree emergence and establishment may be expected in different years (Nilsson *et al*. 2002).

2.5 Acknowledgements

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Chapter 3

Effects of herbaceous neighbours and cattle grazing disturbance on first-year tree seedling establishment

Charlotte Vandenberghe

Abstract

Competition from plant neighbours and herbivory can both affect establishment chances for tree individuals and subsequently the dynamics of highly biodiverse mixed woody-herbaceous plant systems. This study tested for the interactive effects of competition from plant neighbours and cattle grazing on germination, emergence, survival and growth of four native tree species sown in a pasture in the Swiss Jura Mountains. The competition treatment existed out of an herbicide application and the grazing treatment existed out of 3 cattle grazing exposures (no, delayed and continuous). Fate of the emerged seedlings was followed during one year.

Germination and seedling emergence were facilitated by presence of vegetation for all species, except *Picea*, whereas overall survival and growth were inhibited by competition. Cattle activity (*i.e.* browsing, trampling and dunging) affected negatively emergence and survival but not growth. The presence of cattle decreased invertebrate and rodent interaction with tree seedlings. Highest mortality occurred in competition with neighbours under highest cattle grazing intensity. Grazing did slightly change interactions between neighbours and seedlings for seedling survival but not for emergence and growth. A decreased competition effect was found under delayed grazing treatment since seedlings in gaps were more susceptible to cattle activity. Establishment chances decreased with increasing cattle intensity and were highest for *Picea*, intermediate for *Abies* and *Acer* and lowest for *Fagus*. Since establishment in ungrazed conditions stayed lower than 30 %, biotic and abiotic factors other than large herbivore grazing are also important in impeding first-year tree seedling establishment in wood-pastures.

Keywords: emergence, gaps, germination, herbicide, herbivory, mountain wood-pasture, seedling survival, sowing, trampling, tree regeneration

3.1 Introduction

Both competition from plant neighbours and herbivory can affect the survival and growth of new trees and therefore will affect the abundance and composition of tree populations (Harper 1977; Hambäck and Beckerman 2003). Understanding the relative importance of herbaceous interference and ungulate herbivory on tree establishment is fundamental to understand dynamics and maintenance of mixed woody-herbaceous plant systems driven by large herbivores such as wood-pastures (Olff *et al.* 1999).

Plants may resist herbivore damage by escape, defence or tolerance. Their resistance also changes with ontogenetic stage (Boege and Marquis 2005). Abiotic stress, invertebrates and rodents represent main barriers for tree recruitment during seed and seedling stage (≤ 1 year) whereas large herbivores were often found to be the most important factor inhibiting tree establishment during the saplings stage (± 1 - 8 years) (Putman 1986; Smit *et al.* 2002, Vandenberghe *et al.* in press a; Vandenberghe *et al.* in press b; Smit *et al.* 2006). However, few experimental studies quantified the influence of large herbivores on the seed and seedling stage (but see Smit *et al*. unpublished data a). Large herbivores directly modify seed germination and seedling recruitment by consumption (with or without herbaceous neighbours), dunging or trampling damage (Winkel *et al.* 1991; Griscom *et al.* 2005) but also have indirect effects through disturbance of the ground vegetation (*cf.* gap creations), increasing soil compaction, changing seed- and seedling-predator abundances and reducing plant competition (Karl and Doescher 1993; Trimble and Mendel 1995; Smit *et al.* 2001; Jurena and Archer 2003; Vazquez and Simberloff 2003; Goheen *et al.* 2004).

The interaction between herbaceous vegetation and tree seedlings may shift from competition to facilitation under changing abiotic or biotic stress conditions (Gill and Marks 1991; Burton and Bazzaz 1995; Cornett *et al.* 1998; Davis *et al.* 1999; Mazia *et al.* 2001; Nilsson *et al.* 2002; Agestam *et al.* 2003; Brooker *et al.* 2006). For example, vegetation may inhibit seedling establishment in years with normal moisture regimes but facilitate it in dry years when the vegetation may maintain a moist microclimate (DeSteven 1991a; Berkowitz *et al.* 1995). Vegetation cover may inhibit seedling establishment through providing a more protective habitat for seed and seedling predators (Ostfeld and Canham 1993; Vandenberghe *et al.* in press b) or facilitate through reduced detectability of seeds (DeSteven 1991a). Herbivory has been found to increase or decrease plant competition (McPherson 1993; Hambäck and Beckerman 2003; del-Val and Crawley 2005). In pastures, cattle may reduce competitive effects through herbaceous biomass removal (Karl and Doescher 1993). On the other hand, grazed seedlings may be poorer competitors (Meiners and Handel 2000). Moreover, the ability of different tree species to compete is expected to vary due to their growth rate and seed size as well as their resistance to grazing (Young and Young 1992; Moles and Westoby 2004). Furthermore, the relationships among woody seedling establishment, gaps in the sward and the behaviour of predators may be species dependant (Gill and Marks 1991; Roy and Bergeron 1990; Hjälten *et* *al.* 2004).

We performed a factorial field experiment testing for two factors, cattle grazing and competition from neighbours, for each of the four most common tree species in wood-pastures of the Swiss Jura Mountains. The overall hypothesis was that the competitive effects of herbaceous neighbours on woody species establishment in pastures would differ along a cattle grazing intensity gradient. The following specific questions were addressed: How do competition from neighbours and cattle grazing activity affect tree seed germination, seedling emergence, survival and growth? Is the magnitude of the competition effect by neighbours the same under different grazing intensity treatments?

3.2 Methods & Materials

3.2.1 Study site

A traditionally managed pasture (2.25 ha) in the Swiss Jura Mountains (Les Verrières, 6°27'26" E, 46°56'22"N, altitude 1125 m a.s.l.) was used. The pasture is surrounded by a beech-fir forest of the *Abieti-Fagenion* (Delarze *et al.* 1998) and has been grazed during spring and summer by cattle for decades under a rotational grazing system. The mean June temperature in 2004 (12.6 °C ± 3.8 (SD)) and 2005 (14.6 °C ± 4.9 (SD)) was slightly lower and higher respectively, than normal (1994-2003 average: 13.0 ± 2.2 (SD)). Total precipitation of 2004 (1248 mm) and 2005 (1175 mm) was lower than normal (1994-2003: 1607 mm ± 548 (SD)). The sward is dominated by *Festuca rubra* and *Agrostis capillaris*, and the soils are rich in clay (30%), acidic ($5.5 < pH < 6.0$), locally hydromorphic, and belong to the brown-soil class (Neyroud 1993). In 2004, between May and October, the pasture was grazed four times for about 10 days by a herd of 14 18-month-old steers or a stocking rate of 198 Livestock Unit Days ha^{-1} (1 Livestock Unit = 600 kg cattle weight).

3.2.2 Experimental design

A factorial field experiment involving cattle grazing (3 levels), competition from neighbours (2 levels) and species (4 levels) was conducted from May 2004 till June 2005. Four blocks of 48 m x 4 m were randomly laid out within the pasture, spaced at least 60 m from each other (Appendix 3). Each block was divided into three plots of 4 m x 9.5 m, and three grazing treatments were randomly assigned to the plots: a plot submitted to zero grazing ("ZG"), delayed grazing ("DG") and continuous grazing ("CG") were spaced 8 m from each other. Each grazing plot was divided into 4 sub-plots of 2 m x 4 m, spaced at 0.5. Each sub-plot consisted of 8 sowing plots of 25 cm x 25 cm at 1m spacing; sowing plots were used as the experimental unit. Competition (2 levels) and species (4 levels) treatments were randomly assigned to sowing plots. There were a total of 384 sowing plots.

The ZG plots were protected from cattle grazing using an electric fence. The DG plots were protected from cattle grazing for the first 3 months of the experiment. The CG plots were accessible to cattle during the four grazing periods of 2004. The resulting grazing intensity as measured by Livestock Unit Days ha^{-1} was 0 for ZG, 120 for DG, and 198 for CG. In 2005, none of the plots were grazed by cattle. Competition from neighbours was reduced (further called "gap") using a glyphosate herbicide (Round up) which was applied one month before sowing the seeds. During growing season 2004, the withered plants were removed with a rake and re-growing herbs were cut monthly by hand at soil level and removed. Vegetation was left intact in half of the sowings plots (further called "no gap"). The ZG plots contained an extra sub-plot, controlling for natural seed fall and used for microclimate measurements in gaps and no gaps.

3.2.3 Seed and seedling measurements

We used the seeds of the four most common tree species of the Jura Mountains as targets: the evergreen species *Picea abies* (160 seeds/gram) and *Abies alba* (23 seeds/gram) and the deciduous species *Acer pseudoplatanus* (11 seeds/gram) and *Fagus sylvatica* (4.6 g/seed) (nomenclature of plants follows Lauber and Wagner (2000)). We bought seeds harvested from regional montane sites at altitudes similar to those of the field site from a local nursery (Lobsigen, Switzerland). Seeds were cold-stratified (4°C) in wet sand to break seed dormancy, for two (*Fagus*), five (*Acer*) or eight (*Abies*) weeks (Burkart 2000) until one day before sowing. The wings of the *Acer* seeds were cut off to avoid them being displaced by the wind. Forty (*Picea*, *Acer* and *Fagus*) or 80 *(Abies*) seeds were sown per sowing plot at the end of May 2004. Seeds sown on bare soil were slightly covered with soil in order to prevent displacement by wind. Seeds sown into intact vegetation were placed on the soil surface without disturbing the roots of the vegetation. Sowing took place under rainy weather conditions. Also in May, seed germinability was tested using 240 seeds of each species in a greenhouse pot experiment with a randomised design and was defined as the number of seedlings emerged x (number of seeds $sown)^{-1}$.

After two, three and four months and after one year, seed germination and emergence was recorded and the fate of each emerged individual was monitored. A seed was noted as germinated if a green part outside the seed coat was visible. A seedling was noted as emerged if it had developed its cotyledons. Individuals were marked by placing coloured tooth-picks next to the seedling, using a different colour for each observation period. The cause of death was noted as: 1) cattle, if seedlings were browsed (leaves or wood parts were ripped off), trampled or covered with dung, 2) predation, if seedlings showed gnawed-off stems or leaves due to insects, slugs or rodents (*Arvicola terrestris* L. and *Microtus arvalis* L.) or, if a seedling was missing but vole faeces or mounds were present and 3) competition, if seedlings were desiccated, rotten or not found. Since it was difficult to distinguish rodent and insect damage (especially for evergreen species) these causes were analyzed together. All live seedlings were harvested in June 2005, individually oven-dried and weighed to determine total biomass.

Due to significant differences in germinability among species in the greenhouse trial (germination rates: *Abies* 22%, *Picea* 55 %, *Acer* 52 %, *Fagus* 66 %), field germination, emergence and establishment rates were corrected for germinability, *i.e*. the number of sown seeds were multiplied by the proportion of seed germinability. Seed germination was calculated per sowing plot as: (total number of germinated seeds) x (corrected number of sown seeds)$^{-1}$ (total number = sum over all observations). Seedling emergence was calculated per sowing plot as: (total number of emerged seedlings) x (corrected number of sown seeds)$^{-1}$. Seedling establishment was based on number of seedlings present in a sowing plot at final observation, divided by the corrected number of sown seeds. Survival proportion was calculated per sowing plot as: (number of seedlings at harvest) x (total number of emerged seedlings)$^{-1}$ and could not be computed for sowing plots with zero emergence. We calculated the percentage of seedlings that died due to cattle, predation and competition for each treatment as: (number of dead seedlings for each cause of death) x (total number of dead seedlings)$^{-1}$ x 100. Only live seedlings were used in computing total seedling biomass (g) per sowing plot.

3.2.4 Microclimate conditions

Environmental conditions were characterized at the scale of individual sowing plots in ZG plots. Photosynthetically active radiation (PAR (µmol m^{-2} s^{-1}), 400-700 nm) reaching the soil surface was measured simultaneously in a randomly chosen gap and no gap and repeated three times in each of the four ZG plots (n = 12). Measurements were carried out in May 2005 using a Li-COR (LI-1400) radiometer (LI-COR, Quantum sensor, Lincoln, Nebraska, USA). Air temperature and humidity and surface soil temperature and moisture were measured during both growing seasons in May and June, by placing a sensor (Campbell Scientific, Markasub AG, Olten, Switzerland) for each variable in two "gaps" and two "no gaps" in the additional sub-block of one randomly chosen ZG plot. All sensors were connected with a Campbell data logger. Measurements were made synchronously at 15-min intervals. The sensor measuring air temperature and humidity was placed at about 15 cm above ground level. Surface soil moisture was measured using gypsum blocks (Campbell Scientific, Markasub AG, Olten, Switzerland) in 2004 but not in 2005 due to technical problems. In 2005, soil samples were collected to 10 cm depth in each block in one randomly selected gap and no gap of both ZG and CG plots (n = 16). Soil moisture contents were then calculated in the laboratory as: % water = ((wet weight– dry weight) x dry weight)$^{-1}$ x 100.

3.2.5 Data analysis

All statistical analyses were done with R, version 2.1.1 (R Foundation for Statistical Computing, 2004). Since significant interactions between species, grazing and competition were found, analyses were separated by species.

A linear mixed-effects split-plot model with resistricted maximum likelihood estimation (REML, Pinheiro and Bates 2000) was used to analyze the fixed effects of grazing and competition and their interaction on seedling emergence, establishment and biomass. Response variables emergence and establishment were arcsin transformed and biomass was log transformed to reduce heteroscedasticity. Block was included as random factor, grazing as whole plot factor and competition as split plot factor.

Grazing and competition effects and their interaction on sapling survival were tested with a Chi-square likelihood ratio using a logistic regression. A generalised linear model (GLM) with a binomial distribution and logit link function was fitted to the survival data. The response variable was a two-column matrix representing the number of live and dead saplings for each sowing plot and species (Venables and Ripley 2002). Because block effects are difficult to interpret in a GLM with categorical data, we did not use mixed-effects models. GLM is a hierarchical statistical method, meaning that variables are added sequentially. Block (d.f. 3) was included as the first explanatory variable, which controls for block effects when testing the significance of factors.

The influence of grazing and competition on the causes of death (cattle predation and competition) was analyzed with a 3-way contingency table. We combined causes competition and cattle for testing differences between ZG, DG and CG plots since both causes depended on treatments and cattle could not be a cause of death in ZG. Consequently, we tested separately for the effect of 3 causes of death between DG and CG which both could have cattle as cause of death. We used a GLM with a poisson distribution and log link function, with percentage of dead saplings as response and three categorical factors (cause of death, grazing and competition) and their interactions as explanatory variables. Significance was assessed using the difference in deviance between the generalised linear models with and without the corresponding interaction using the “drop” function in R (Venables and Ripley 2002).

3.3 Results

3.3.1 Microclimate conditions

Photosynthetically active radiation in gaps at the soil surface was significantly higher than in no gaps (Table 3.1). Overall, gaps were warmer and drier although absolute differences were small (Table 3.1).

Table 3.1 Abiotic conditions (means ± 1 SE) measured in ungrazed plots: air temperature, air humidity, soil temperature, soil humidity and photosynthetically active radiation, in gaps and no gaps for the growing seasons of 2004 and 2005. Different letters indicate statistically different values per year and variable (Kruskal-Wallis; $P < .05$).

			Gap	No gap
temp air	(°C)	2004	12.3 ± 0.08^{a}	12.3 ± 0.08^{a}
		2005	11.9 ± 0.09^{a}	11.8 ± 0.09^{a}
hum air	(%)	2004	87.2 ± 0.20^{a}	88.7 ± 0.19^{b}
		2005	83.8 ± 0.18^{a}	84.1 ± 0.19^{b}
temp soil	(°C)	2004	13.1 ± 0.04^{a}	12.4 ± 0.02^{b}
		2005	11.7 ± 0.05^{a}	11.0 ± 0.03^{b}
hum soil	(bar)	2004	2.63 ± 0.02^{a}	2.94 ± 0.03^{b}
	(%)	2005	51 ± 3.6^{a}	54 ± 4.4^{a}
PAR	(µmol m^{-2} s^{-1})	2005	1709 ± 89.4^{a}	400 ± 60^{b}

3.3.2 Seedling germination and emergence

In 70 of the 384 sowing plots (10, 11, 14, and 35 for *Picea, Abies*, *Acer,* and *Fagus* respectively) no seedlings emerged. Most seedlings emerged during the first 2 observations (*i.e.* 2 and 3 months after sowing). For *Picea*, *Abies*, *Acer* and *Fagus* respectively 1, 6, 1 and 1 newly emerged seedlings were observed during the third observation (*i.e.* 4 months after sowing). One year after sowing, 6, 0, 3 and 3 newly emerged seedlings were observed for *Picea, Abies*, *Acer* and *Fagus* respectively. Germination and emergence percentages differed between species (Table 3.2). Forty percent of the germinated *Fagus* seeds did not develop cotyledons. Except for *Picea*, seedling emergence was significantly lower in gaps (Table 3.3a), with 19 %, 16 % and 5 % reduction for respectively *Abies*, *Acer* and *Fagus*. No consistent trend was found for *Picea*. Emergence rate was not different in ZG and DG plots but tended to be lower in CG plots (Fig. 3.1), although differences were significant only for *Abies* and *Acer*. For all species continuous grazing (compared to ZG) reduced emergence, by 17 %, 20 %, 8 % and 4 % for *Picea, Abies*, *Acer* and *Fagus* respectively.

Table 3.2 Corrected overall germination, emergence, survival and establishment percentages (mean ± 1 SE, n = 96) of the four tree species. Establishment represents the final number of seedling present in plots.

	Picea	*Abies*	*Acer*	*Fagus*
Germination	40 ± 2.9	31 ± 2.3	21 ± 1.7	13 ± 1.4
Emergence	40 ± 2.9	28 ± 2.3	19 ± 1.6	8.0 ± 0.9
Survival	32 ± 3.2	28 ± 3.5	40 ± 4.1	23 ± 4.3
Establishment	16 ± 2.1	8.9 ± 1.3	7.4 ± 1.1	2.1 ± 0.4

Table 3.3 Results of the linear mixed-effects model (REML) for the effects of grazing and competition and their interaction on *a*) seedling emergence and *b*) seedling establishment for each of the four species (n = 96); response variables were arc sinus transformed.

		Picea		*Abies*		*Acer*		*Fagus*	
a) Emergence									
Grazing	$F_{2,6}$	0.69	ns	5.87	*	5.56	*	1.56	ns
Competition	$F_{1,81}$	0.17	ns	38.2	****	40.1	****	12.7	***
G x C	$F_{2,81}$	1.45	ns	0.48	ns	0.05	ns	0.27	ns
b) Establishment									
Grazing	$F_{2,6}$	1.27	ns	6.78	*	3.83	ms	3.65	ms
Competition	$F_{1,81}$	10.3	**	0.54	ns	0.75	ns	0.05	ns
G x C	$F_{2,81}$	1.91	ns	0.67	ns	0.14	ns	2.16	ns

$P < .05$*; $P < .01$**; $P < .001$***; $P < .0001$****; ms: $.05 < P < .1$; ns: non significant result.

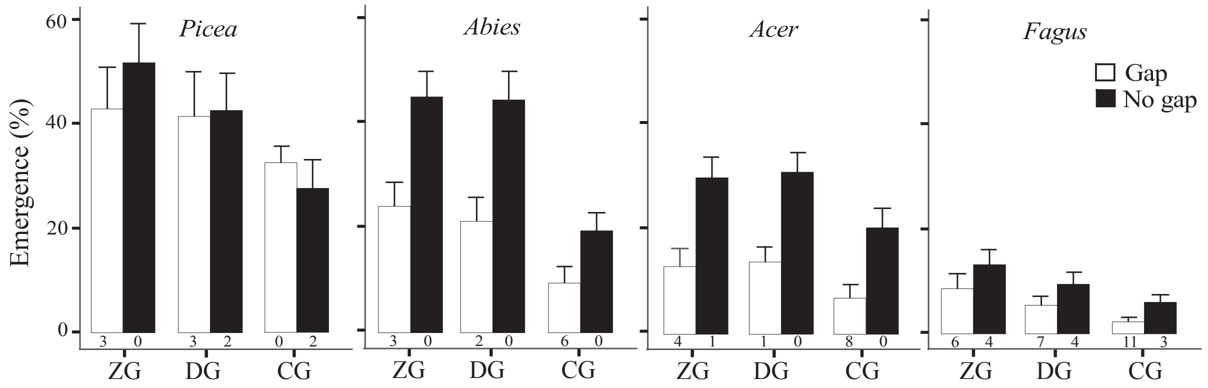

Figure 3.1 Seedling emergence percentage for each of the four tree species in gaps (white bars) and no gaps (black bars), in zero grazing (ZG), delayed grazing (DG) and continuously grazing (CG) plots. Data presented are means (± 1 SE, *n* = 16). Letters indicate the number of sowing plots without seedling emergence.

3.3.3 Seedling survival

Survival percentages differed between species (Table 3.2). For all species, survival was lowest in no gaps of CG plots and was highest in gaps of ZG plots (Fig. 3.2). Competition negatively affected survival in all grazed plots except for *Fagus* in DG plots. For *Picea*, continuous cattle activity significantly increased the competitive effect whereas delayed cattle grazing exposure reduced it (interaction G x H, Table 3.4). The same tendency was found for *Acer* (Fig. 3.2).

Table 3.4 Results of the logistic regression (GLM with binomial distribution and logit link) for the effects of the grazing and competition and their interaction on seedling survival for each of the four tree species.

		Picea *n*=86		*Abies* *n*=85		*Acer* *n*=82		*Fagus* *n*=61	
	df	χ^2		χ^2		χ^2		χ^2	
Grazing	2	13.4	**	13.3	**	16.7	***	4.62	ms
Competition	1	44.7	****	4.46	*	15.3	****	5.96	*
G x C	2	15.5	***	1.52	ns	1.69	ns	8.88	*

$P < .05$*; $P < .01$**; $P < .001$***; $P < .0001$****; ms: $.05 < P < .1$; ns: non significant result.

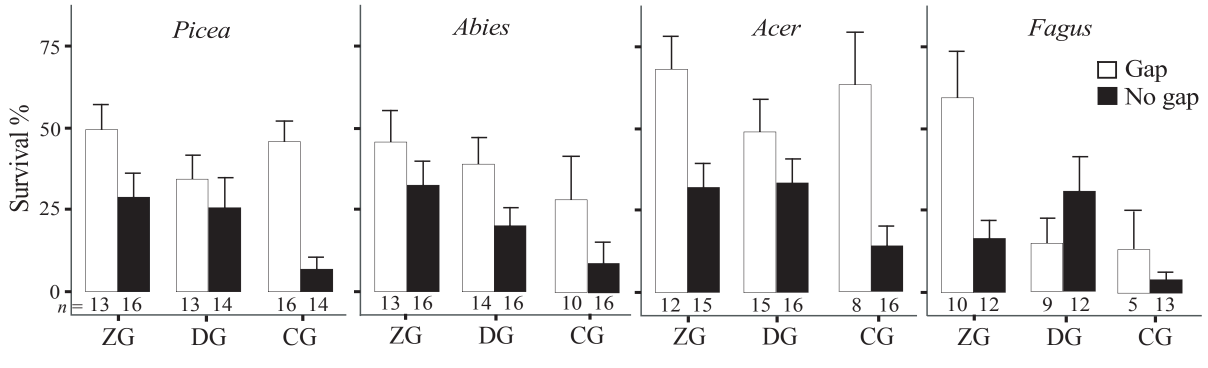

Figure 3.2 Final seedling survival percentage for each of the four tree species in gaps (white bars) and no gaps (black bars) in zero grazing (ZG), delayed grazing (DG) and continuously grazing (CG) plots. Data presented are means (± 1 SE).

For *Picea* and *Acer*, herbicide had a larger positive effect (respectively 22 % and 33 %) than total cattle exclusion (ZG) (respectively 10 % and 17 %). For *Abies* and *Fagus*, cattle exclusion had a greater relative positive effect (respectively 22 % and 29 %) than herbicide (respectively 18 % and 16 %). Negative response to cattle activity occurred immediately but was weak for *Picea*. Competition from neighbours decreased survival of *Picea* and *Acer* more rapidly than for *Abies* and *Fagus* (Fig. 3.3).

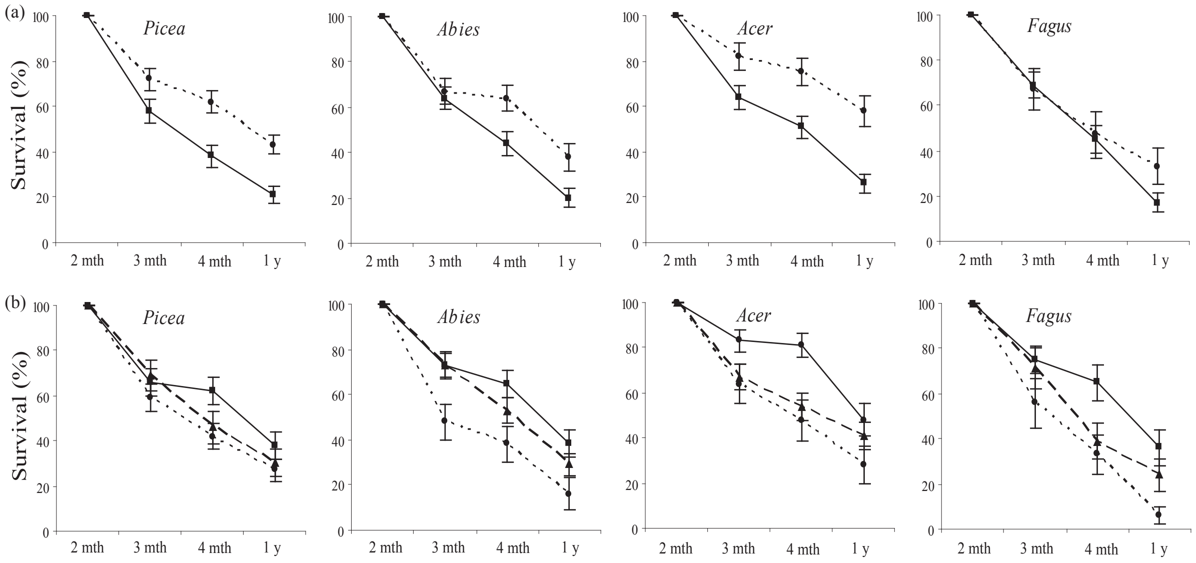

Figure 3.3 Seedling survival percentage for each of the four tree species and after 2, 3 and 4 months and 1 year, a) in gaps (dotted line) and no gaps (solid line) and b) in zero grazing (ZG, solid line), delayed grazing (DG, dashed line) and continuous grazing (CG, dotted line) plots. Data presented are means (± 1 SE), based on (number of seedlings present) x (total number of emerged seedlings)$^{-1}$ per sowing plot and at each observation period. Note the variation in duration between observation dates.

The relative proportion of seedlings that died due to predation by invertebrates and rodents decreased with increasing grazing exposure (Fig. 3.4; cause (2 levels) x grazing: *Picea*: $\chi^2 = 35$, d.f. 2, $P < .0001$; *Abies*: $\chi^2 = 57$, d.f. 2, $P < .0001$; *Acer*: $\chi^2 = 221$, d.f. 2, $P < .0001$; *Fagus*: $\chi^2 = 169$, d.f. 2, $P < .0001$). For *Abies*, invertebrate and rodent predation was more important in gaps (cause (2 levels) x competition: $\chi^2 = 27$, d.f. 1, $P < .0001$). For *Picea*, *Acer* and *Fagus*, cattle damage was more important in gaps (cause (3 levels) x competition: *Picea*: $\chi^2 = 9.1$, d.f. 2, $P < .05$; *Acer*: $\chi^2 = 69$, d.f. 2, $P < .0001$; *Fagus*: $\chi^2 = 8.3$, d.f. 2, $P < .05$).

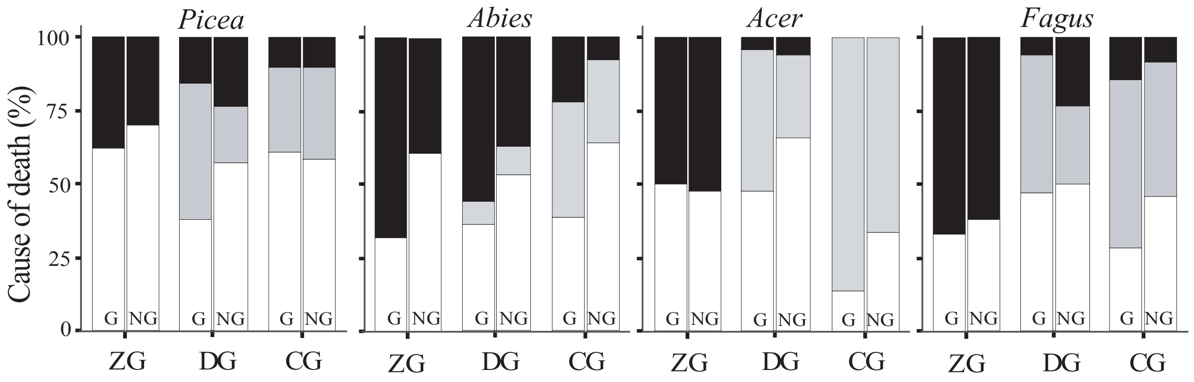

Figure 3.4 Cause of seedlings death (%) with black bars representing proportion of seedlings that died due to insect or rodent predation, grey bars due to cattle activity and white bars due to desiccation or not found; for each species, in gaps (G) and no gaps (NG), and in zero grazing (ZG), delayed grazing (DG) and continuously grazing (CG) plots.

3.3.4 Seedling growth

Seedling growth was highly significantly favoured in gaps for all species (Table 3.5, Fig. 3.5). No significant differences between the grazing plots and no significant interactions were found for any of the species. After 12 months, the evergreen species, and in particular *Picea*, were smaller than the deciduous species (Fig. 3.5).

Table 3.5 Results of the linear mixed-effects model (REML) for the effects of grazing and competition and their interaction on seedling biomass for each of the four species; response variables were log transformed.

	Picea *n =57*			*Abies* *n = 49*			*Acer* *n = 54*			*Fagus* *n = 24*		
Grazing	$F_{2,5}$	1.59		$F_{2,5}$	0.92		$F_{2,6}$	0.74		$F_{2,2}$	1.08	
Competition	$F_{1,43}$	39.0	****	$F_{1,35}$	30.4	****	$F_{1,39}$	26.4	****	$F_{1,13}$	12.8	**
G x C	$F_{2,43}$	0.99		$F_{2,35}$	1.91		$F_{2,39}$	0.43		$F_{2,13}$	0.41	

P < .05*; *P* < .01**; *P* < .001***; *P* < .0001****; ms: .05 < *P* < .1; ns: non significant result.

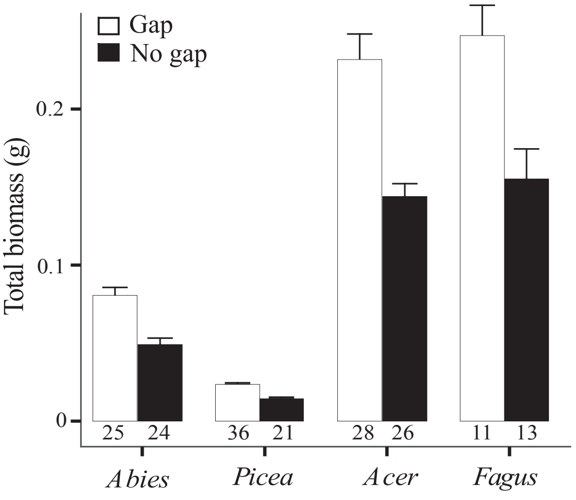

Figure 3.5 Total seedling biomass for each of the four tree species in gaps (white bars) and no gaps (black bars). Data presented are means (± 1 SE, *n* is noted). No significant differences were found between the zero grazing (ZG), delayed grazing (DG) and continuously grazing (CG) plots.

3.3.5 Seedling establishment

Seedling establishment can be seen as a combination of emergence and survival rates. Gaps had a significantly positive effect on *Picea* seedling establishment but for the other species, the low emergence in gaps led to a net negative effect (Table 3.3b, Fig. 3.6a). Seedling establishment gradually decreased with increasing cattle disturbance although cattle relatively limited establishment never more than 13 % (Fig. 3.6b). At the end of the experiment, *Fagus* had the lowest number of seedlings (Table 3.1). Excluding (ZG) and delaying (DG) cattle grazing positively influenced establishment but not significantly for *Picea* (Table 3.3b, Fig. 3.6b). Grazing (CG) reduced establishment for *Picea*, *Abies*, *Acer* and *Fagus* by 13 %, 12 %, 7 % and 3 % respectively.

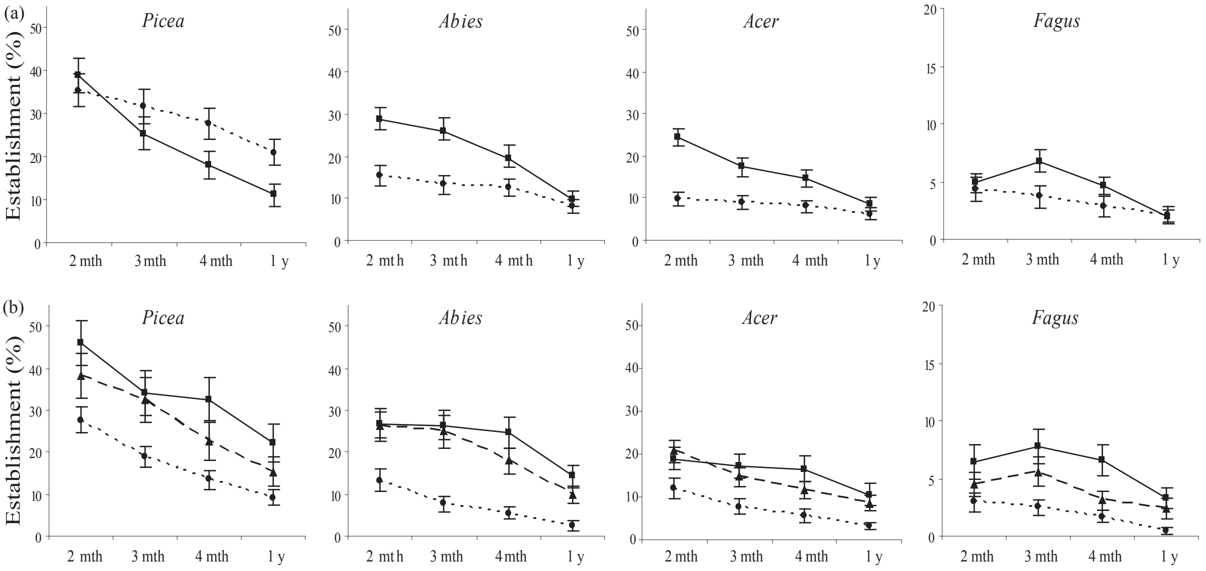

Figure 3.6 Seedling establishment percentage for each of the four tree species in a) gaps (dotted line) and no gaps (solid line) and in b) zero grazing (ZG, solid line), delayed grazing (DG, dashed line) and continuous grazing (CG, dotted line) plots. DG plots were accessible to cattle after 3 months. Data presented are means (± 1 SE), based on (number of seedlings present) x (corrected number of sown seeds)$^{-1}$ per sowing plot and at each observation period. Note change of scale for *Fagus* and variation in duration between observation dates.

3.4 Discussion

3.4.1 Germination and emergence

Germination and seedling emergence were facilitated by presence of vegetation for all species except *Picea*, which is in contrast with the frequently observed competitive suppression by established herbaceous vegetation (Gill and Marks 1991; Nilsson *et al.* 2002; Agestam *et al.* 2003). Ameliorated microclimate conditions in the intact vegetation might have caused the facilitative interaction (DeSteven 1991a; Berkowitz *et al.* 1995) although the growing season of 2004 was not particularly warm or dry. The competition effect on emergence might have been swamped out by post-dispersal seed predation (Cornett *et al.* 1998) although we did not track the fates of individual seeds. The vegetation might have protected seeds from discovery by visually oriented foragers such as birds (DeSteven 1991a; Nystrand and Granström 1997). Rodents, granivorous insects and slugs were also potential seed predators at our field site but avoid normally foraging in open areas (Ostfeld and Canham 1993; Hulme 1997; Nystrand and Granström 2000; Vandenberghe *et al.* in press b). Moreover, gaps tended to have more often zero seedling emergence (Fig. 3.1) which might be explained by density-dependant seed predation (Hulme and Borelli 1999).

Cattle negatively affected emergence rates during the first three months after sowing, through trampling or burying the seeds deep in the soil. However, seeds might have been displaced from the plots through trampling and germinated elsewhere. Grazing did not change the facilitative interactions between neighbours and seedling emergence.

The deciduous species showed overall a lower germination and emergence rate than the evergreen species. Next to a higher seed predation risk due to a greater energetic value and visibility (Jennings 1976; Hulme and Borelli 1999; Smit 2002), they might had more difficulties to emerge in vegetation due to desiccation of the radicle before penetrating the soil since they make less soil contact than small seeds (personal observation).

3.4.2 Seedling survival and growth

In contrast with effects on emergence, competition from neighbours decreased seedling survival (DeSteven 1991b; Gill and Marks 1991; Rawlinson *et al.* 2004). The highest mortality occurred in the presence of competition under the highest cattle grazing intensity (Meiners and Handel 2000; Griscom *et al.* 2005). One of the tendencies observed was a reduced competition effect on survival under delayed cattle grazing exposure but increased competition effect under continuous cattle grazing (Fig. 3.2). The emerged seedlings in the gaps of the delayed grazing plots (*i.e.* protected from cattle for 3 months after sowing) represented a greater and more visible proportion of biomass compared to continuously grazed plots, probably increasing their susceptibility to cattle herbivory (DeSteven 1991b; Ashby 1997; Griscom *et al.* 2005). Cattle negatively affected seedling survival via browsing, trampling or dunging (Jimenez *et al.* 2005; Li *et al.* 2003; personal observation). In contrast to the deciduous species, the direct effects of cattle on coniferous seedlings were more often a result of trampling or dunging rather than browsing since seedlings were generally shorter than the grazing height.

Although the distinction between rodent and invertebrate damage was difficult to make, we observed that deciduous species were more susceptible to predation by rodents which might be due to their low phenolic levels (Roy and Bergeron 1990; Hjälten *et al.* 2004) and large size (Hulme 1994) whereas needles and cotyledons of coniferous species were more often attacked by insects or slugs. The proportion of seedlings that died due to rodents and invertebrates was higher under reduced cattle activity, most likely due to enhanced predator population abundances (Smit *et al.* 2001; Goheen *et al.* 2004). Rodent and invertebrates did not forage preferably on seedlings in intact vegetation as found by several studies (Ostfeld and Canham 1993; Hulme 1997; Vandenberghe *et al.* in press b, Smit *et al.* in press). *Abies* was even more susceptible to invertebrate and rodent predation in gaps than in intact vegetation. It might be that the small seedlings were more easily found in gaps.

When protected from cattle grazing, large-seeded species *Acer* and *Fagus* had higher survival in the gaps than evergreen species, probably due to greater seed reserves in combination with a long taproot (Moles and Westoby 2004). However, this was no longer an advantage in presence of neighbours. For *Fagus*, other effects such as predation and an overall rapid seedling mortality in pastures most probably masked the competition effect which became significant only after winter (unreported analyses; Fig. 3.3a). Seedlings of slow growing evergreen species have high desiccation risks (Griscom *et al.* 2005) and their survival rate was higher than found previously during a warm and dry year (Vandenberghe *et al.* in press b).

Seedling growth was negatively affected by neighbours but not by grazing. Seedling tolerance to cattle activity is very low due to limited resources of seedlings (Boege and Marquis 2005), often resulting in death after damage. Consequently, seedlings still alive at harvest were not or poorly affected by cattle and did not suffer from biomass losses. Contrary, older saplings, which are more tolerant, persist at least in the short term with reduced biomass (Griscom *et al.* 2005; Vandenberghe *et al.* in press a). Light levels were higher in gaps and likely positively affected growth (Mazia *et al.* 2001; Löf *et al.* 2004; Vandenberghe *et al.* in press b). Gaps were also warmer and drier but this did not negatively influence seedling growth, which suggests that soil water availability was not limiting.

3.4.3 Tree establishment and ecological implications

Establishment in pastures was highest for *Picea*, intermediate for *Abies* and *Acer* and lowest for *Fagus*. The establishment advantage of *Picea* seedlings might explain why it is the most common tree species in the wood-pastures of the Swiss Jura Mountains (Gallandat *et al*. 1995). Competition from neighbours negatively affected only *Picea* seedling establishment. However, the positive effect of gaps on establishment was masked by the lower emergence rate in gaps for *Abies*, *Acer* and *Fagus*. The positive effects of gaps on survival in combination with cattle exclusion as found in this study may however become negative in time since natural gaps in ungrazed swards will build-up more litter and revegetate faster than those in pastures, resulting in complex gap – seedling interactions (Bullock *et al.* 1995).

Seedling establishment in ungrazed conditions stayed below 30 % (*i.e.* based on the corrected numbers for germinability). Besides overall low chances for tree seeds to make it to seedlings (Farmer 1997), many interacting biotic (*e.g.* neighbours and predators such as large herbivores, rodents and invertebrates) and abiotic (*e.g.* moisture and light) factors are responsible for impeding first-year tree seedling establishment in wood-pastures. More precise insight on the habitat-specific impact of different consumers on tree seedling emergence and survival, during different years and weather conditions, should be obtained via the use of selective exclosures, insecticide and fungicides as carried out in short-term for predation by insects, rodents, birds and cattle of *Picea* by Smit *et al.* (unpublished data a).

3.5 Acknowledgements

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Chapter 4

Short-term effects of cattle browsing on tree sapling growth in mountain wooded pastures

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Abstract

Browsing by livestock has been identified as an important factor preventing tree regeneration in wooded pastures. Two field experiments were performed to investigate the effects of cattle browsing on tree sapling growth in a mountain wooded pasture. Two size classes (ca. 12 - 17 cm and 41 - 59 cm) of each of 4 species (*Picea abies*, *Abies alba*, *Acer pseudoplatanus* and *Fagus sylvatica*) were exposed to zero, low and high grazing intensities. We measured the proportion of saplings browsed and the effect of browsing on growth. A mowing treatment within the zero grazing intensity treatment showed no significant effect on sapling growth. One percent of the large saplings but 25% of the small saplings escaped browsing. Saplings were better protected when surrounded by taller vegetation. The proportion of saplings browsed was not significantly different among species although evergreen tree saplings lost a larger proportion of biomass than deciduous species when browsed. Under grazing, average current-year shoot production and total aboveground biomass of all species were significantly reduced. Browsing effects tended to be smaller at the lower grazing intensity. Because the deciduous species were least reduced in aboveground growth, especially under the low grazing intensity, we conclude that at least in short-term, deciduous species are less affected by cattle browsing.

Keywords: *Abies alba*, *Acer pseudoplatanus*, competition, *Fagus sylvatica*, grazing intensity, *Picea abies*, silvopastoral system, tree regeneration

4.1 Introduction

In recent decades, agricultural intensification has reduced the area occupied by ancient wooded pastures in temperate Europe. Several examples remain, including in the Swiss Jura Mountains. To conserve these landscapes, trees and herbaceous vegetation must be able to continue to coexist in a dynamic equilibrium under livestock grazing (Vera 2000; Archer *et al.* 2001). Worldwide, land managers are increasingly interested in combining silviculture and agriculture to re-establish silvopastoral systems, in order to preserve biodiversity and provide socio-economically viable options for local farmers (Etienne 1996; Hobbs and Yates 2000; Teklehaimanot *et al.* 2002). Young trees are vulnerable to browsing and understanding the factors affecting their establishment is of concern (Gillet and Gallandat 1996; Sharrow *et al.* 1992). If grazing intensity is too high, trees fail to regenerate and wooded pastures evolve towards grassland ecosystems. In absence of pastoral activities, they evolve towards climax forest ecosystems. Livestock foraging behaviour in grasslands and rangelands has been an area of intensive research (Rook *et al.* 2004) but the effect of livestock on biomass of woody species in the herb layer has received much less investigation.

Cattle generally select for a grass-based diet with a high digestibility and high N and P concentrations (Ayantunde 1999; Mayer *et al.* 2003). Due to the high levels of difficult-to-digest lignin and secondary metabolites, most woody species are generally avoided by cattle (Gordon 2003). However, browsing by livestock has been identified as an important factor preventing tree regeneration in wooded pastures (Papachristou and Papanastasis 1994; Lehmkuhler *et al.* 2003; Bakker *et al.* 2004; Allcock and Hik 2004). The consumption of woody plants increases when high quality forage is unavailable, often under dry weather conditions (Holechek *et al.* 1982; Owen-Smith and Cooper 1987; Fritz *et al.* 1996) or in late summer (Leloup *et al.* 1996). Tree sapling damage and mortality also increases with grazing pressure (Pitt *et al.* 1998; Hall *et al.* 1992), a result of increased consumption or trampling. In the wooded pastures of the Swiss Jura Mountains, four common tree species, including two conifers (*Abies alba* and *Picea abies)* and two deciduous species (*Acer pseudoplatanus* and *Fagus sylvatica*), co-occur between an altitude of 800 and 1200 m. *Picea abies* is currently dominant. Little is known about the selectivity of domesticated cattle among these different species and the responses of saplings to browsing. Apparency, *i.e.* the probability that an individual plant will be discovered by its enemies (Feeny 1976), is not only dependant on the characteristics of the plant itself, e.g. plant size, foliage abundance and duration (Welch *et al.* 1991; Zamora *et al.* 2001; Renaud *et al.* 2003) but also on the relative abundance and nature of neighbouring plants (Milchunas and Noy-Meir 2002). Coniferous species are likely to be more apparent than deciduous species, but might be avoided by cattle because of their lower leaf nitrogen content (Pagès *et al.* 2003) and stiff, tough needles. Furthermore, deciduous species have a greater ability for compensatory growth after browsing damage because conifers store most of their nutrients in the needles, whereas deciduous species have greater stores in roots and old wood (Chapin *et al.* 1990; Hester *et al.* 2004).

Livestock will consume not only saplings but also the surrounding vegetation. Tree sapling success may be strongly influenced by the intensity of competition from herbaceous vegetation (e.g. Gill and Marks 1991; Pagès *et al.* 2003). Livestock may, therefore, have an indirect positive effect on tree sapling establishment at sites where grazing reduces the ability of grasses to competitively exclude less-preferred woody seedlings (Archer 1995).

The effect of cattle on the growth of tree saplings of different species under varying grazing intensities has, to our knowledge, never been quantified in wooded pastures. The relative importance of the direct (biomass removal) and indirect (reduced competition) effects of cattle browsing on sapling growth is not well known. In this research, our first objective was to quantify direct browsing effects. We investigated if the probability of being browsed depended on species, sapling size, grazing intensity or the height of the surrounding vegetation. Furthermore, we quantified the reduction in sapling growth due to cattle browsing and examined differences in sapling growth between species, sapling sizes and grazing intensities. Our second objective was to assess the strength of indirect grazing effects using a mowing experiment.

4.2 Methods & Materials

4.2.1 Study site and focal species

Two field experiments were conducted over the growing season of 2003 in two adjacent paddocks of a site called ‘La Petite Ronde’ (6°27’26” E, 46°56’22”N, altitude 1125 m a.s.l.) at Les Verrières in the Swiss Jura Mountains, which is rented by the Agroscope-Changins and Liebefeld-Posieux Research Institutions (Switzerland). The site has been grazed for more than 100 years and a rotational grazing system was established in 2000. In 2003, between May and October, each paddock was grazed four times for approximately 15 days by a herd of 22 18-month-old steers. The year 2003 was particularly hot and dry with a mean June temperature of 18 ± 2.2 (SD) °C (1994 – 2003 mean June temperature 13 ± 2.2 °C) and a total of 980 mm of precipitation (1994 – 2003 mean 1607 ± 548 mm). The most common herbaceous species were *Festuca rubra, Agrostis capillaris*, *Cynosurus cristatus, Alchemilla xantochlora* aggr., *Prunella vulgaris, Trifolium repens. Centaurea jacea* s.l. and *Ranunculus acris friseanus* (nomenclature follows Lauber and Wagner 2000). The site was surrounded by a mixed forest and tree saplings were observed in adjacent paddocks. However, all naturally established tree saplings in the paddocks had been mechanically removed by the farm managers in former years.

We used the four most common tree species of the wooded pastures of the Jura Mountains: the evergreen species *Picea abies* and *Abies alba* and the deciduous species *Acer pseudoplatanus* and *Fagus sylvatica*. Tree saplings of two sizes were obtained from a local nursery (Lobsigen, Switzerland) and were transplanted into two paddocks exposed to different intensities of grazing.

Table 4.1 Age, initial height, diameter and initial dry mass (mean ± 1 SE) of the small and large transplanted tree saplings (*n*=128 per species). Regression formulas used to estimate initial aboveground dry mass (DM, g) from height (h) and basal diameter (d) measures on the four species and two size classes. For all models, $n = 18$ and $P < .001$.

Species	Size	age (y)	height (cm)	diam (cm)	initial DM (g)	log(DM) =	R^2
Abies	small	3	12.6 ± 0.3	0.27 ± 0.01	0.69 ± 0.12	$-0.156 + 0.732 \times \log(d^2h)$	0.905
	large	6	40.6 ± 0.9	1.13 ± 0.04	34.9 ± 21.1	$0.035 + 0.859 \times \log(d^2h)$	0.865
Picea	small	2	12.3 ± 0.3	0.23 ± 0.01	0.67 ± 0.38	$-0.031 + 0.900 \times \log(d^2h)$	0.875
	large	5	50.6 ± 1.1	1.13 ± 0.03	50.6 ± 23.1	$0.256 + 0.790 \times \log(d^2h)$	0.910
Acer	small	1	18.6 ± 0.6	0.31 ± 0.01	0.42 ± 0.19	$-0.543 + 0.604 \times \log(d^2h)$	0.810
	large	3	58.8 ± 1.2	0.65 ± 0.02	4.1 ± 1.6	$-0.138 + 0.659 \times \log(d^2h)$	0.798
Fagus	small	1	16.8 ± 0.5	0.34 ± 0.01	0.54 ± 0.33	$-0.556 + 0.838 \times \log(d^2h)$	0.886
	large	3	57.1 ± 1.1	0.75 ± 0.02	6.7 ± 2.4	$-0.288 + 0.753 \times \log(d^2h)$	0.700

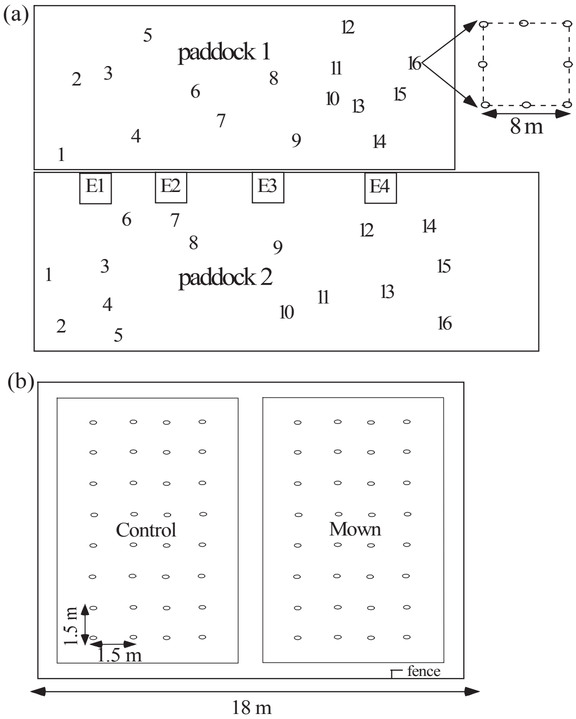
4.2.2 Experimental design

Two experiments were carried out: a browsing experiment tested for direct browsing effects and a mowing experiment for indirect effects. The height and diameter (at 1 cm above root collar) of all experimental saplings were measured before transplantation in mid-April 2003 (Table 4.1). 'Small' and 'large' sapling size classes were defined by height rather than age. Eighteen additional saplings of each species and size class were measured, dried at 60°C for 48h, and weighed. These data were used to construct a linear regression model for each species in order to estimate the initial aboveground biomass of the experimental saplings (Table 4.1). Saplings that died due to transplantation shock or late frost (2 small and 3 large *Abies*, 3 small *Picea*, 19 small *Acer* and 14 small and 6 large *Fagus*, total of 47 of 512 saplings) were replaced one week before cattle arrived in both paddocks on 27 May 2003.

For the browsing experiment, trees were transplanted into two paddocks of different grazing intensities. Paddock 1 (3.3 ha) had a high grazing intensity with a stocking rate of 128 Livestock Unit Days ha^{-1} and paddock 2 (4.5 ha) had a lower grazing intensity with a stocking rate of 94 Livestock Unit Days ha^{-1} (1 Livestock Unit = 600 kg cattle weight). Sixteen blocks (8 m x 8 m) of 8 saplings were randomly placed into each paddock (total of 256 saplings) (Fig. 4.1a, Appendix 4). Within each block, saplings (4 species x 2 sizes) were randomly assigned to positions and planted at the mid-points and corners of each block (Fig. 4.1a). This resulted in a minimum distance of 4 m between saplings. Mean vegetation height (± 1 SE) before the arrival of cattle was 11.5 ± 2.8 cm in paddock 1 and 11.8 ± 2.9 cm in paddock 2. After two rotation periods, mean vegetation height was 7.6 ± 1.8 cm in paddock 1 and 8.9 ± 1.9 cm in paddock 2. The mean aboveground dry mass in July was 118 g m^{-2} for paddock 1 and 125 g m^{-2} for paddock 2. The factor "grazing intensity" could not be replicated due to logistic constraints and the paddock and grazing intensity effects are therefore confounded. However, we believe that the grazing intensity effect is much larger than the paddock effect as the two paddocks were adjacent and similar in vegetation, slope and soil type (Vandenberghe unpublished data).

For the mowing experiment, four 15.5 m x 18 m exclosures (used as statistical blocks), were erected in paddock 2, adjacent to the border with paddock 1 (Fig. 4.1a). Each exclosure was split into two plots of 13.5 x 7.5 m surrounded by a 1 m buffer zone: in a randomly selected plot, vegetation was mown; the other served as a control (Fig. 4.1b; Appendix 4). Each plot contained 4 individual saplings of each combination of species and size class (4 species x 2 sizes x 4 replicates: 32 saplings) randomly assigned to positions. A total of 256 saplings were transplanted (32 individuals x 2 plots x 4 exclosures). In the mown plots, vegetation around the saplings was cut to about 3 cm with a grass hand-mower and removed on 16 May, 30 May, 4 June, 25 June and 15 July. In the control plot, mean vegetation height (± 1 SE) in July was 15.6 ± 3.0 cm and mean aboveground dry mass was 360.5 g m^{-2}.

Figure 4.1 (a) Experimental layout: 16 blocks were randomly located in paddock 1 (high grazing intensity) and paddock 2 (low grazing intensity). Each 64 m^2 block (shown in expanded view) consisted of 8 saplings (○ = sapling) randomly assigned to positions within the block. Four exclosures (E) were erected in paddock 2. (b) In each of the exclosures, saplings were randomly assigned to positions within plots.



4.2.3 Data collection

In the browsing experiment, each sapling was examined in the field and scored as browsed or unbrowsed after each grazing period. The height of the vegetation surrounding each sapling was measured before (HB) and after (HA) the first grazing period with a herbometer (Mosimann *et al.* 1999). A plastic sheet (30 cm x 30 cm, 344g) was lowered onto the canopy along a plastic rod and the height at which it came to rest was used as a measure of overall vegetation height. Vegetation height was measured at 4 points adjacent to each sapling in the cardinal directions and averaged. The absolute and relative reductions in vegetation height (ΔH = [HB-HA] and $\Delta Hrel = \Delta H \times HB^{-1}$) were calculated. The saplings of the browsing experiment were harvested on 4-5 August 2003, *i.e.* after two grazing periods of 14 days and 17 days, respectively. All saplings were cut at the root collar and scored as either dead or alive, based on the presence of green fibres under the cortex. Live saplings were separated into new growth and previous years' growth. The parts were oven-dried for 48h at 60°C and weighed. Saplings that were pulled out by cattle (4 % of the large and 22 % of the small saplings) were scored as browsed but excluded from growth analyses.

Saplings of the mowing experiment were harvested on 15-16 August 2003. Sapling survival was scored and the final dry weight of live saplings was calculated as in the browsing experiment. One small sapling of each of *Fagus* and *Acer* could not be relocated and one large *Abies* was browsed by roe deer (*Capreolus capreolus*) and excluded from the analysis.

We focussed on two measures of sapling growth: (1) NG: relative new growth, calculated as the ratio of current-year shoot biomass over initial aboveground biomass and (2) BC: biomass change, calculated as the ratio of final over initial aboveground biomass. Sapling survival at the time of harvest was not analysed as we expected sapling death to continue due to browsing stress.

4.2.4 Statistical analyses

All data were analyzed with R, version 2.1.1 (R Foundation for Statistical Computing 2004). We used mixed effect models using blocks as random factors to account for within-paddock variability. Individual trees, clustered within blocks, were treated as independent sampling units since we assumed that the distance of 4 m between the saplings was sufficient to ensure independence with regard to the probability of being browsed.

A logistic regression was performed to test the effects of species, grazing intensity and size class on the probability of being browsed. Estimations were performed using generalized linear mixed effects models estimated by maximum likelihood procedures (glmmML, Broström 2005). Likelihood ratio tests were applied to test significance of predictor variables. The complete model with 3 fixed factors and all pairwise interactions could not be estimated because the number of parameters was too large. The interaction terms were therefore tested separately, adding each of them to a model including only statistically significant main effects.

The relationships between predictor variables "overall vegetation height" (HB), "absolute height reduction by grazing" (ΔH), "relative height reduction by grazing" (ΔHrel), "grazing intensity" (G) and "size class" (S) and the response variable "probability of a sapling being browsed during the first grazing period" were tested using glmmML procedures. We tested all pairwise interactions independently. Species was excluded because no significant species effect on browsing frequency was found in the previous analysis.

We tested for an effect of grazing intensity and size class on NG and BC. Sapling growth was analysed separately for each species because growth rates vary between species. Response variables were log-transformed to reduce heteroscedasticy (log (NG + 1) and log BC) and a normal distribution was assumed. Analyses were conducted using linear mixed effect models (LME, Demidenko 2004) fitted by likelihood maximization. The use of LME models is more reliable than conventional ANOVA when analysing unbalanced data (Pinheiro and Bates 2000). Significance of the predictor variables was tested by comparing the fit of full and reduced models using likelihood ratio tests.

We tested for a mowing effect on NG and BC with mowing treatment, size class and their interaction as fixed predictors, using LME models and likelihood ratio tests as described for the browsing experiment. Exclosures were treated as a random factor.

Finally, in order to quantify the degree of growth reduction under grazing we combined data from the two experiments. We compared the NG and BC for saplings exposed to grazing to those in exclosures. We built a new predictor variable, grazing intensity, with three categories: zero, low and high. Given there was no detectable mowing effect, we included all saplings within exclosures at the zero grazing level. As previously, we used LME procedures on log (NG + 1) and log (BC). Blocks (browsing experiment) and exclosures (mowing experiment) were combined and used as random factors.

4.3 Results

4.3.1 Browsing experiment

After the first grazing period, 66 % of the saplings were browsed under low grazing intensity against 78 % saplings under high grazing intensity (L-ratio = 5.28, d.f. 1, $P = 0.022$). The browsing frequency between large (98 %) and small saplings (46 %) differed significantly (L-ratio = 108.1, d.f. 1, $P < .0001$) (Fig. 4.2a). No differences between species were found (L-ratio = 4.37, d.f. 3, $P = 0.22$). Few small *Fagus* saplings were browsed in the paddock with the lower grazing intensity but the interactions species x grazing intensity (L-ratio = 4.36, d.f. 3, $P = 0.22$) and grazing intensity x size were not significant (L-ratio = 1.32, d.f. 1, $P = 0.25$). After the second grazing period, the proportion of tree saplings browsed under low grazing intensity (85 %) and high grazing intensity (89 %) no longer differed significantly (L-ratio = 1.0, d.f. 1, $P = .32$) (Fig. 4.2b). The difference between tree size classes remained significant (Fig. 2b, 99 % of large vs. 75 % of small saplings, L-ratio = 41.2, d.f. 1, $P < .0001$). The four species were browsed at approximately the same ratio (L-ratio = 2.37, d.f. 3, $P = 0.49$).

The probability of a sapling being browsed decreased with increasing height of surrounding vegetation (HB: L-ratio = 6.55, d.f. 1, $P = 0.01$) (Fig. 4.3). In contrast, the probability of a sapling of being browsed was not significantly related to either absolute or relative reduction in vegetation height (ΔH: L-ratio = 2.67, d.f. 1, $P = 0.10$; ΔHrel: L-ratio = 0.12, d.f. 1, $P = 0.73$). No significant interactions between vegetation height variables, grazing intensity (G) and size class (S) were found (d.f. 1 for all tests; HB x S: L-ratio = 0.5, $P = 0.5$; ΔH x S: L-ratio = 3.9, $P = 0.06$; ΔHrel x S: L-ratio = 0.2, $P = 0.7$; HB x G: L-ratio = 2.6, $P = 0.1$; ΔH x G: L-ratio = 0.5, $P = 0.5$; ΔHrel x G: L-ratio = 3.2, $P = 0.07$).

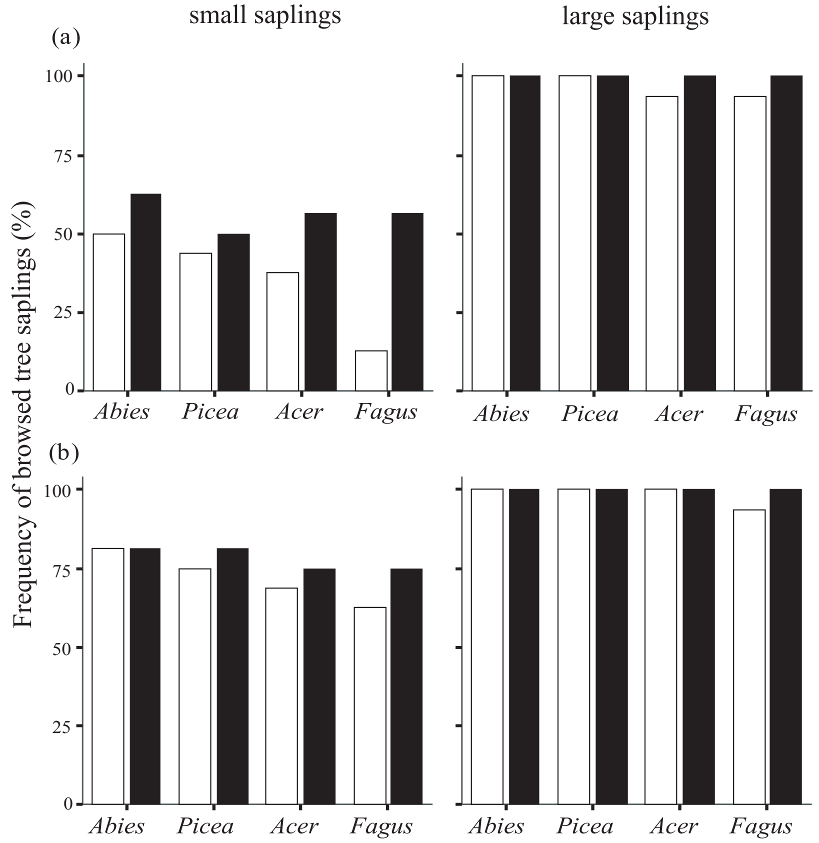
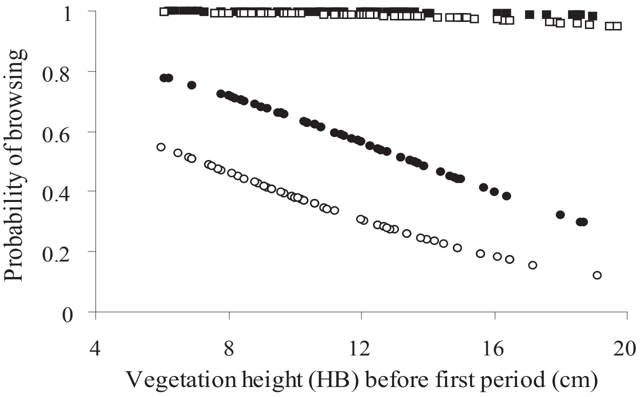


Figure 4.2 Percentage of saplings browsed after the (a) first and (b) second grazing period for each tree species, size class and level of grazing intensity (white bars: low grazing intensity, black bars: high grazing intensity).

Figure 4.3 Estimated probabilities (using logistic regression with a logit link) of each individual sapling being browsed as a factor of surrounding vegetation height (HB), controlling for effects of size class (○: small saplings and □: large saplings) and grazing intensity (unfilled symbols: low grazing intensity and filled symbols: high grazing intensity).



The G x S interactions were not significant for NG or BC (Table 4.2). The difference between low and high grazing intensity was significant only for *Acer* growth, but small saplings of all species tended to have greater NG under low grazing intensity (Fig. 4.4). For *Picea*, *Acer* and *Fagus*, small saplings produced relatively more new biomass (NG) than large saplings but aboveground biomass change (BC) did not differ significantly between sizes, except for *Abies*. In contrast to the evergreen species, all *Acer* and small *Fagus* saplings increased their aboveground biomass compared to their initial biomass under low grazing intensity, but not under high grazing intensity. Deciduous species were relatively less affected than evergreen species, which lost up to half of their initial biomass (Fig. 4.5).

Table 4.2 Browsing experiment: likelihood ratio tests (L-ratio) for effect of grazing intensity (low and high), tree size class and their interaction (G x S) on relative new growth (log (NG + 1) and aboveground biomass change (log BC) of saplings.

	Abies *n*=45			*Picea* *n*=48			*Acer* *n*=50			*Fagus* *n*=48		
	L.Ratio	df		L.Ratio	df		L.Ratio	df		L.Ratio	df	
NG												
Grazing	0.01	1	ns	1.43	1	ns	4.5	1	*	2.33	1	ns
Size	2.45	1	ns	4.33	1	*	9.85	1	**	6.33	1	*
GxS	2.82	1	ms	1.85	1	ns	3	1	ms	2.98	1	ms
BC												
Grazing	0.23	1	ns	0.01	1	ns	8.43	1	*	0.31	1	ns
Size	10.7	1	*	0.02	1	ns	3.52	1	ms	2.22	1	ns
GxS	0.7	1	ns	0.08	1	ns	1.3	1	ns	2.55	1	ns

$P < .05$*; $P < .01$**; $P < .001$***; $P < .0001$****; ms: $.05 < P < .1$; ns: non significant result.

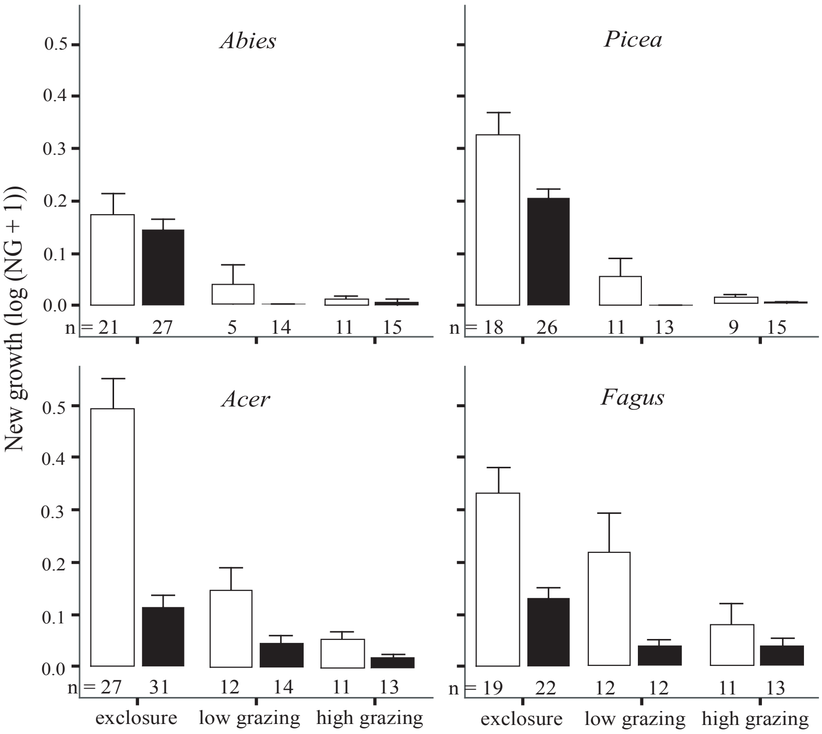
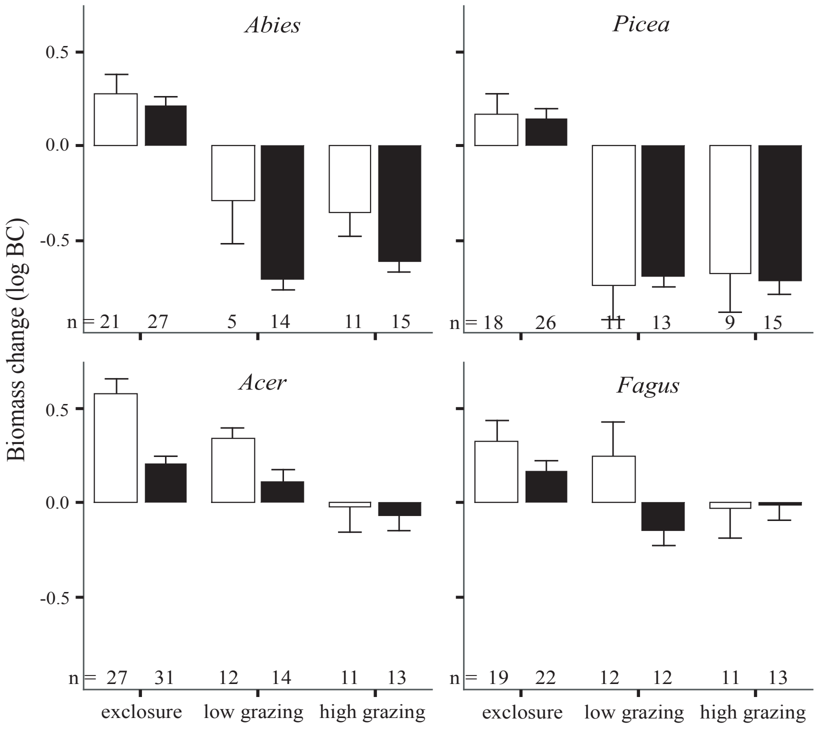


Figure 4.4 Effect of grazing intensity (zero, low and high) and tree size class (white bars: small saplings; black bars: large saplings) on relative new growth (log (NG + 1)) (± 1 SE) for each of the four tree species.

Figure 4.5 Effect of grazing intensity (zero, low and high) and tree size class (white bars: small saplings, black bars: large saplings) on aboveground biomass change (log BC) (± 1 SE) for each of the four tree species. Negative values correspond to biomass decrease, positive values to biomass increase.



4.3.2 Mowing experiment

The mowing treatment had no significant effect on NG and BC for either large or small saplings for any species (Table 4.3). Small saplings produced relatively more current-year shoots than large ones, except for *Abies* (Table 4.3, Fig. 4.4).

Table 4.3. Mowing experiment: likelihood ratio tests (L-ratio) for the effect of mowing, tree size class and their interaction (M x S) on relative new growth (log (NG+1)) and aboveground biomass change (log (BC)) of exclosed saplings.

	Abies *n*=48			*Picea* *n*=44			*Acer* *n*=58			*Fagus* *n*=41		
	L.Ratio	df		L.Ratio	df		L.Ratio	df		L.Ratio	df	
NG												
Mowing	0.87	1	ns	0.38	1	ns	0.37	1	ns	0.97	1	ns
Size	0.65	1	ns	7.38	1	**	32.6	1	****	14.3	1	****
MxS	0.48	1	ns	0.68	1	ns	0.56	1	ns	0.13	1	ns
BC												
Mowing	0.78	1	ns	0.24	1	ns	0.27	1	ns	0.64	1	ns
Size	0.42	1	ns	0.01	1	ns	17.4	1	****	1.76	1	ns
MxS	0.22	1	ns	0.40	1	ns	0.14	1	ns	0.05	1	ns

$P < .05$*; $P < .01$**; $P < .001$***; $P < .0001$****; ms: $.05 < P < .1$; ns: non significant result.

4.3.3 Combined analysis

The combined analysis provided evidence for significant reduction in growth due to cattle browsing compared to ungrazed control saplings although the effect was only marginally significant for BC of *Fagus*. One significant interaction was found for NG of *Acer* saplings (Table 4.4). Percentage reduction of new growth reached up to 99 % for coniferous species (Table 4.5). For deciduous species the mean new growth reduction was lower (71 %). Aboveground biomass was reduced on average with 54 % for conifers and 22 % for deciduous species compared to growth of saplings in ungrazed situations. It was relatively lowest for *Fagus* (6 % for small saplings under low grazing intensity) (Table 4.5).

Table 4.4 Combined analysis: likelihood ratio tests (L-ratio) for grazing intensity (zero, low, high), for tree size class and their interaction (G x S) on relative new growth (log (NG+1)) and aboveground biomass change (log BC) of saplings.

	Abies	*n*=93		*Picea*	*n*=92		*Acer*	*n*=108		*Fagus*	*n*=89	
	L.Ratio	df		L.Ratio	df		L.Ratio	df		L.Ratio	df	
NG												
Grazing	23.7	2	****	38.9	2	****	23.3	2	****	11.9	2	*
Size	1.07	1	ns	10.2	1	*	36.3	1	****	19.5	1	****
GxS	0.33	2	ns	4.19	2	ns	21.3	2	****	4.60	2	ns
BC												
Grazing	40.1	2	****	24.3	2	****	22.1	2	****	5.20	2	ms
Size	6.24	1	*	0.01	1	ns	19.1	1	****	3.93	1	*
GxS	3.60	2	ns	0.11	2	ns	4.65	2	ms	2.93	2	ns

P < .05*; *P* < .01**; *P* < .001***; *P* < .0001****; ms: .05 < *P* < .1; ns: non significant result.

Table 4.5 Percentage reduction in relative new growth (% NG) and aboveground biomass change (% BC) of small and large saplings exposed to low and high grazing intensities.

	low grazing		high grazing	
	small	large	small	large
% NG				
Abies	80	99	95	95
Picea	84	99	97	99
Acer	76	61	92	83
Fagus	33	72	79	72
% BC				
Abies	43	61	48	57
Picea	56	57	55	57
Acer	26	10	44	24
Fagus	6	26	27	16

% BC = [(mean BC_control – mean BC_grazing) x (mean BC_control)$^{-1}$] x 100

% NG = [(mean NG_ control – mean NG_grazing) x (mean NG_control)$^{-1}$] x 100

4.4 Discussion

The probability of a sapling being browsed depended on its size and the height of surrounding vegetation but not on its species. Saplings were more likely to be grazed early in the season under higher grazing intensity. By the end of the browsing experiment, only one large sapling but one quarter of the small saplings had escaped browsing. More frequent browsing of large saplings may be due to the greater apparency of saplings with more biomass. Similar effects have been found for other herbivores and tree species (Palmer and Truscott 2003; Renaud *et al.* 2003). Small saplings, which have smaller root systems, were more often uprooted and thus less persistent than large ones. However, uprooting occurred mainly after the first grazing period, when root fixation after transplantation was probably not yet complete.

The probability of the saplings of being browsed by cattle was lower when the surrounding vegetation height was high, as has been found elsewhere (DeSteven 1991b; Zamora *et al.* 2001). This protection tended to be more effective in the paddock subjected to the lower grazing intensity. If we suppose that the saplings were browsed by chance together with the surrounding vegetation, then the observed effect of vegetation height may mean that (1) for morphological reasons the chance of a sapling being included in the bite is smaller when surrounding vegetation is taller or (2) cattle spent more time in patches where vegetation is short (WallisDeVries *et al.* 1999). Because cattle are primarily grazers (Gordon 2003), the rate of sapling discovery should depend on the perceived value of a particular patch in which the sapling is located. If the neighbourhood of the tree sapling is attractive, they are more likely to be browsed (Rousset and Lepart 2003). Tree regeneration has been shown to occur most often in safe sites (Harper 1977), such as on rocky outcrops or near unpalatable plants providing protection against browsers (Callaway *et al.* 2000; Milchunas and Noy-Meir 2002; Bakker *et al.* 2004; Smit *et al.* 2005).

Overall, browsing reduced both the biomass of current-year shoots (NG) and total aboveground biomass (BC) for all tree species and size classes. In addition to being browsed, almost all large saplings showed clear basal scarring due to trampling (pers. obs. C.V.) (*cf.* Pitt *et al.* 1998), but none of the saplings were broken. This study was conducted under unusually dry weather conditions and the amount of browse consumed by cattle is likely to vary with weather conditions and forage availability (Pollock *et al.* 2005). Although statistically significant only for *Acer*, all small saplings tended to have a higher new growth production under low grazing intensity than under high grazing intensity, as has been found for birch saplings exposed to sheep grazing (Hester *et al.* 1996). Although small saplings escaped more often browsing than large ones, they did not show in all cases a lower relative reduction in biomass (Table 4.5). Small saplings lost relatively a larger proportion of biomass when effectively browsed than large ones.

The evergreen species we used lost relatively more biomass when browsed than the deciduous species. The larger reduction was presumably due to a more vulnerable plant architecture and the attractive abundant fresh foliage at the start of the summer (Welch *et al.*

1991). Moreover, deciduous species may more quickly compensate for mammalian herbivory by mobilizing stored energy reserves from stem and roots for refoliation (Chapin *et al.* 1990; Hester *et al.* 2004). Small *Fagus* saplings seemed to be less reduced in biomass when exposed to browsing than the other species. This might be partly explained by a lower browsing frequency during the first grazing period (Fig. 4.4), allowing more biomass production before being damaged. The differences in biomass losses do not necessarily imply a lower survival rate for conifers although tolerance to defoliation is generally greater in deciduous than coniferous species (Krause and Raffa 1996). The performance of the deciduous species may decline in later growing seasons, especially if their resources have been depleted to compensate for damage but also due to repeated browsing.

Unexpected findings emerged from the mowing experiment since reducing aerial biomass around the saplings did not affect sapling growth. Competition for light between grasses and planted tree saplings may have been outweighed by belowground competition for resources. In contrast, Gill and Marks (1991) found that aboveground competition with herbs reduced tree sapling growth more severely than belowground competition. In their study, water was not a limiting factor which may have increased the relative importance of light. The extremely warm and dry weather conditions during the growing season of 2003 may have increased the importance of water and thus weakened the effect of light competition. As suggested by Nilsson and Örlander (1995), after they found no effect of sward mowing on *Picea* sapling growth, the evaporative demand of the planted saplings may have been higher in mown plots since control saplings were partly shaded. Furthermore, mowing may have altered the availability of other resources such as soil nitrogen (Holland and Detling 1990) and understanding the multiple effects of mowing will require further experiments. In addition, the duration of our experiment (3 months) may not have been long enough to detect competition effects. Browsing and plant competition interactions might be expected (see Husheer *et al.* 2006) because the reduction of aboveground surrounding vegetation by herbivores may also increase the probability of being browsed (Canham *et al.* 1993; see above) and/or affect browsing tolerance (Weltzin *et al.* 1998; Wise and Abrahamson 2005).

We have showed that browsing frequency depends on the tree size and the height of surrounding vegetation but not on species. Cattle browsing reduced tree sapling growth of the four most common tree species of the wooded pastures in the Swiss Jura Mountains. The differences in browsing frequency and sapling growth between low and high grazing intensities were moderate. At least in the short term, the deciduous species were less affected in aboveground growth and thus more tolerant at this particular stage than the evergreen species. In order to survive, tree saplings must be browsing tolerant, i.e. they should be able to persist at least temporarily with reduced biomass and to compensate for biomass loss through active regrowth. To determine which species is most tolerant over longer terms, we are studying the effects of herbivory on whole-sapling growth and survival in an experiment currently underway.

4.5 Acknowledgements

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Chapter 5

Interactive effects of simulated summer browsing, shade and herbaceous neighbours on tree sapling tolerance

Charlotte Vandenberghe, François Freléchoux and Alexandre Buttler

Abstract

The ability of saplings to tolerate browsing is influenced by intrinsic (morphological and physiological) factors and extrinsic factors such as environmental resources available for growth. However, few studies have investigated the interactions between multiple environmental factors on sapling responses to browsing for different species. We applied simulated cattle summer browsing, shade and above-ground competition removal treatments to two deciduous (*Acer pseudoplatanus* and *Fagus sylvatica*) and two coniferous (*Picea abies* and *Abies alba*) tree species to examine survival and whole-sapling biomass responses after two-growing seasons.

The negative effect of neighbours on sapling performance was enhanced under shade. *Picea* was least and *Abies* most competition tolerant. None of the clipped saplings fully compensated for biomass losses due to simulated browsing. Simulated browsing reduced survival and growth of *Picea* and *Acer* more than for *Abies* and *Fagus*. *Picea* showed lowest compensatory growth response and was the only species which was not negatively affected by strong irradiance of a mountain pasture. For all species, the positive effect of neighbours on compensatory growth responses tended to be higher under shade. Tolerance was increased under conditions which negatively affected plant growth probably due to the fact that the biomass change needed to compensate was smaller. The degree of browsing tolerance was not related to plant performance as saplings that compensated almost for clipping damage still had a lower overall growth.

At least in the short term, browsing sapling damage will have minor impacts in situations with intense competitive interactions such as reduced grazing intensities. Full sun conditions as found in open mountain wood-pastures are not required for maximum performance in the juvenile stage of tree species which are sensitive to strong irradiance or hold traits for indirect facilitation by shade.

Keywords: *Abies alba*, abiotic factors, *Acer pseudoplatanus*, cattle, compensatory growth, competition, clipping, *Fagus sylvatica*, mowing, *Picea abies*, tolerance, tree establishment

5.1 Introduction

Wood-pastures are highly biodiverse systems in which large herbivores drive vegetation dynamics through the creation and maintenance of complex assemblages of grassland, shrub and woodland patches. The formation of shifting mosaics in these systems is also driven by the alternation of plant competitive and facilitative interactions (Olff *et al*. 1999; Gillet *et al*. 2002; Bakker *et al*. 2004; Smit *et al*. 2006). Furthermore, interspecific differences in the responses of saplings to browsing, shade and competition tolerance may partly explain community composition dynamics (Gill 1992; Breziecki and Kienast 1994; Canham *et al*. 1994; Walters and Reich 1996; Liang and Seagle 2002; Pagès *et al*. 2003). Insight into the regulatory processes and mechanisms of such mixed woody - herbaceous plant systems and, in particular, the interactions between them, will improve ecological theory and models, in addition to informing management (House *et al*. 2003).

Inhibition of sapling growth and survival in wood-pastures is often related to cattle summer browsing disturbance (Bakker *et al*. 2004; Mayer *et al*. 2005; Vandenberghe *et al*. in press a). Browsing tolerance compromises the ability to persist with reduced biomass and compensate for biomass loss through active regrowth (Strauss and Agrawal 1999; Haukioja and Koricheva 2000). The ability to demonstrate compensatory growth is considered to be lower for conifers mainly because fast-growing deciduous species have more flexible growth patterns and can profit of their ability to mobilize stored energy reserves from stems and roots for refoliation (Millard *et al*. 2001; Ayres *et al*. 2004; Hester *et al*. 2004). Therefore, interspecific differences in intrinsic features promoting browsing tolerance may influence tree composition dynamics. However, saplings in mixed woody – herbaceous plant systems are not exposed solely to browsing, but to several environmental factors simultaneously (House *et al*. 2003).

In forested ecosystems, relationships between light intensity and sapling performance are in general positive (Kozlowski and Pallardy 1997; Grossnickle 2000; Beckage *et al*. 2005). However, sapling performance may improve under shaded conditions, due to direct effects on physiology (photosynthesis, transpiration) (Callaway 1992; Alves *et al*. 2002) or due to indirect effects such as competitive release of herbaceous species (Levine 1999; Siemann and Rogers 2003). Competition from surrounding vegetation generally negatively affects sapling biomass and survival (Peltzer and Köchy 2001; Pagès *et al*. 2003; Allcock and Hik 2004) and can have a greater negative impact than herbivory (Prach *et al*. 1996; Millett *et al*. 2005; Brooker *et al*. 2006). However, neighbourhood vegetation can also play a facilitative role by providing shade and moisture or protection against predators (Gill and Marks 1991).

Interactions between tree browsing tolerance and environmental factors have a fundamental role in determining ecosystem diversity, structure and function. The compensatory continuum hypothesis (CCH) predicts that woody plants have a greater potential for compensatory growth when growing in low-stress, resource-rich environments (Belsky *et al*. 1993; Hjälten *et al*. 1993). As such, limited light availability and competition from neighbours may reduce browsing tolerance (Mclaren 1996; Weltzin *et al*. 1998; Blundell and Peart 2001). However, controversy exist concerning this topic since (over)compensation might also occur under low resource conditions (Hawkes and Sullivan 2001; Puettmann and Saunders 2001; Wise and Abrahamson 2005).

In this study, we measured the survival and whole-sapling biomass responses of two coniferous (*Abies alba* and *Picea abies)* and two deciduous tree species (*Acer pseudoplatanus* and *Fagus sylvatica*) to simulated summer browsing, shade and neighbour removal (mowing) treatments and the interactions between them. The selected tree species have different growth strategies making them interesting species for comparative study involving different environmental conditions from both a research and management perspective. We address the following questions: 1) Are there interspecific differences in responses to neighbour removal, browsing and shading treatments? 2) Do saplings responses to simulated browsing depend on interactions between light availability and the presence of herbaceous neighbours?

5.2 Methods & Materials

5.2.1 Study site and species

The experiment was set up in a calcareous grass-sown sward, situated in the wood-pastures of the Swiss Jura Mountains (La Frétaz, Bullet, 6° 34’ 30” E, 46° 50’ 30” N, 1200 m a.s.l.). The most common species in the sward were *Dactylis glomerata*, *Phleum pratense, Taraxacum officinale, Lolium perenne* and *Agrostis capillaries* (nomenclature follows Lauber and Wagner 2000). The mean July temperature in 2004 and 2005 was respectively 13.8 °C (± 3.7 SD) and 14.7 °C (± 4.1 SD). Total precipitation in 2004 and 2005 was respectively 1374 mm and 1036 mm. Prior to the experiment the sward was mown and grazed by cattle several times during the growing season for 20 years. Rock fragments in subsurface soil were present. We excluded cattle from a 40 m x 40 m area using electric wire to prevent browsing. An additional exclosure, consisted of chicken mesh, was constructed 0.5 m below and above the ground level to decrease the vole population (main species *Arvicola terrestris* L.). Furthermore, within the exclosure, voles were captured with traps (TopCat, Wintersingen, Switzerland) to reduce predation of the saplings.

Saplings of *Picea abies*, *Acer pseudoplatanus*, *Fagus sylvatica* and *Abies alba* (hereafter referred to as *Picea*, *Acer*, *Fagus* and *Abies* respectively) were bought from a local nursery (Lobsigen, Switzerland). They originated from seeds harvested between 700 and 1200 m and had been shaded during previous’ growing season(s). The deciduous saplings *Acer* and *Fagus* were younger than the coniferous saplings *Picea* and *Abies* because of their slower growth rates (Table 5.1).

Table 5.1 Age, initial height, diameter and initial total dry mass (initial DM) (mean ± 1 SE) of the transplanted saplings ($n = 192$ per species). Regression formulas used to estimate initial DM from height (h) and basal diameter (d) measures on the four species, with R^2 value. For all models, $n = 40$ and $P < .001$. Percentage clipped DM (mean ± 1 SE) was calculated as clipped DM x (initial DM)$^{-1}$ of the clipped saplings ($n = 96$).

Species	age (y)	height (cm)	diam (cm)	initial DM (g)	Dry Mass (g) =	R^2	% clipped
Picea	2	12.7 ± 0.2	0.22 ± 0.004	1.25 ± 0.04	$1.057(hd^2)+0.484$	0.77	32.4 ± 0.01
Acer	1	13.0 ± 0.3	0.26 ± 0.003	0.43 ± 0.02	$0.373(hd^2)+0.078$	0.95	19.2 ± 0.01
Fagus	1	19.2 ± 0.3	0.35 ± 0.006	1.39 ± 0.04	$0.372(hd^2)+0.415$	0.84	18.4 ± 0.01
Abies	3	12.9 ± 0.1	0.24 ± 0.004	1.05 ± 0.03	$0.958(hd^2)+0.301$	0.75	32.2 ± 0.01

5.2.2 Experimental design

A factorial field experiment involving shade (shade and no shade), neighbour removal (neighbours and no neighbours), simulated browsing (unclipped and clipped) and species (4, see above) was conducted during two growing seasons (2004 – 2005). The design followed a split plot design (Appendix 5). Six blocks of 14 m x 6 m were laid out within the exclosure over three rows. Each block was divided into two whole plots of each 5 m x 6 m. A plot with shade (S^+) and a plot with no shade (S^-) treatment were randomly assigned within each block. The S^+ plot was spaced 4 m from S^- plot. Each whole plot was divided into two split plots of 2 m x 6 m. A plot with neighbours (N^+) and a plot without neighbours (N^-) were randomly assigned within each whole plot. Within each split plot, 32 saplings (4 species x 4 repetitions) were randomly transplanted over 11 rows and 3 columns and 0.5 m spaced from each other. A clipping treatment was randomly assigned to the saplings. A total of 768 saplings were transplanted in early May 2004. Saplings had been randomized and height and diameter (1 cm above root collar) were measured before planting. Forty additional saplings of each species were measured, oven-dried and weighed. These data were used to construct a linear regression model for each species in order to estimate initial total dry mass (DM) of the experimental saplings (Table 5.1). Saplings that died due to transplantation shock or vole predation, *i.e.* 70, were replaced in early June 2004 and were not considered in the analysis.

Shading treatment: The shade plot (S^+) consisted of a shade tunnel 5 m wide, 6 m long and 2.4 m high in the middle and orientated on a north-south axis. A shade cloth (see Fig. 5.1 for light penetration data) was mounted on a metal frame and draped to 30 cm from the ground on east and west sides. At both north and south ends of the tunnel an extra shade cloth was mounted and fixed to the soil at 2 m outside the tunnel frame and draped 1 m from the ground. This allowed us to transplant saplings over the entire length of the shade tunnel because shade was provided in the tunnel even when the position of the sun was low. The shade cloths were installed at the end of June 2004 and removed in late October 2004 before snowfall. They were reinstalled in April 2005, *i.e.* before the second growing season.

Neighbour removal treatment: In the plots without neighbours (N^-), aboveground herbaceous vegetation surrounding the saplings was mown to ground level at the end of June 2004 and every 4 weeks thereafter. The plots with neighbours (N^+) and the buffer zone of 1 m between the N^- and N^+ plots were left intact.

Simulated browsing treatment: Half of the saplings within each shade x neighbour combination were clipped using scissors. The clipping treatment was designed to mimic as closely as possible cattle browsing damage *i.e.* based on field observations made in previous year for the same species and sapling stage (Vandenberghe *et al.* in press a). Of the *Acer* and *Fagus* saplings we clipped all annual shoots and leaves produced in the current growing season. For *Picea* and *Abies* we clipped half of the shoots produced during the previous growing season, half of the length of branches larger than 1 cm and all shoots produced in the current growing season. The clipping event took place once at the same time of the installation of the shade cloths. The clipped biomass was oven-dried and weighed and percentage clipped DM was calculated (Table 5.1).

5.2.3 Measurements

Photosynthetically active radiation (PAR (µmol m^{-2} s^{-1}), 400-700 nm) was measured at ground level and at 1 m above the herbaceous canopy on a sunny day in September 2004 at midday, with 2 replicates per shade x neighbour combination in all blocks, using a Li-COR (LI-1400) radiometer (LI-COR, Lincoln, Nebraska, USA). Light penetration was calculated as % of incoming light (PAR at ground level x (above canopy PAR in full light)$^{-1}$ x 100). Air temperature and humidity and surface soil temperature and moisture were measured during both growing seasons in July and August, by placing 1 sensor (Campbell Scientific, Markasub AG, Olten, Switzerland) for each variable in each shade x neighbour combination of one block randomly chosen. All sensors were connected to a Campbell data logger (Campbell Scientific, Markasub AG, Olten, Switzerland). Measurements were made synchronously at 15-min intervals. The sensor measuring at the same time air temperature and humidity was placed at about 15 cm above ground level. Surface soil moisture was measured using gypsum blocks. We measured aboveground biomass production of neighbours between S^+ and S^-, by clipping all aboveground biomass in two 0.25-m^2 areas randomly located within all N^- plots 4 weeks after they were mown (August 2005). Herbaceous biomass was oven-dried and weighed.

Survival was determined on 2 occasions in each growing season (July and September). The cause of death was noted as predation when there was an observable damage by voles such as teeth marks on stem, or when roots were predated or when sapling disappeared into a vole gallery exit. Ten saplings were excluded from the dataset because they were mown accidentally. All live saplings were harvested in mid-September 2005 to determine above- and belowground biomass. Roots were extracted from the soil and carefully washed. Saplings were oven-dried and weighed.

Overall growth was calculated only for live saplings as biomass change (BC):

(final DM + clipped DM)/(initial DM)

Clipped DM was added to the final DM to more precisely investigate the effect of simulated browsing on plant growth (Belsky 1986). Saplings that died due to predation were excluded from the survival dataset. Final survival, expressed as percentage, and biomass change were averaged per block (cf. 4 repetitions), for each shade x neighbour combination (6 replicates per treatment). For *Picea*, there were no living unclipped saplings left at the time of harvest in 3 S^+N^+ plots and no living clipped saplings in 2 S^-N^+ and 5 S^+N^+ plots. For *Acer*, 1 S^+N^+ plot did not have living clipped saplings left.

We calculated the compensatory growth response (CG) of the clipped saplings for each shade x neighbour combination as:

BC_clipped saplings/BC_unclipped saplings

(CG >1: overcompensation; CG = 1: compensation and CG < 1: undercompensation)

We used the Relative Neighbour Effect (RNE, Markham and Canway 1996) to analyze the effect of herbaceous neighbours on survival and growth of the four tree species. RNE_values ranged between -1 (competition) and +1 (facilitation) and were calculated per block, for each shade and clipping treatment and each species.

RNE_ Survival was calculated as:

(Survival N^+ – Survival N^-)/highest value

RNE_Growth was calculated as:

(BC N^+ – BC N^-)/highest value

5.2.4 Data analysis

All statistical analyses were done with R, version 2.1.1 (R Foundation for Statistical Computing, 2004).

Non-parametric Kruskal-Wallis tests and Mann-Whitney *U*-tests were conducted to analyze the abiotic factors in each shade x neighbour combination because assumptions for parametric tests were not fulfilled.

The influence of shade, neighbours and clipping on the cause of death (treatment or vole predation) was analyzed with a 4-way contingency table. Therefore, we used a GLM with a poisson distribution and log link function, with number of dead saplings as the response and four categorical factors (cause of death, shade, neighbours and clipping and their interactions). Testing was carried out by using the difference in deviance between the generalised linear models with and without the corresponding interaction using “drop” function in R (Venables and Ripley 2002). Because the saplings were not strictly independent experimental units, the results of this analysis should be viewed as indicative rather than definitive.

Shade, neighbour and clipping effects and their interactions on sapling survival were tested with a Chi-square likelihood ratio using a logistic regression. A GLM with binomial distribution and logit link function was fitted to the survival data. The response variable was a two-column matrix representing the number of survived and dead saplings for each shade x neighbour combination and species (Venables and Ripley 2002). Because block effects are difficult to interpret in a GLM with categorical data, we did not use mixed-effects models. Block was included as the first explanatory variable in the GLM, which is a hierarchical statistical method, meaning that variables were added sequentially. Blocks were not significant for any of the species, and were thus omitted from the final model.

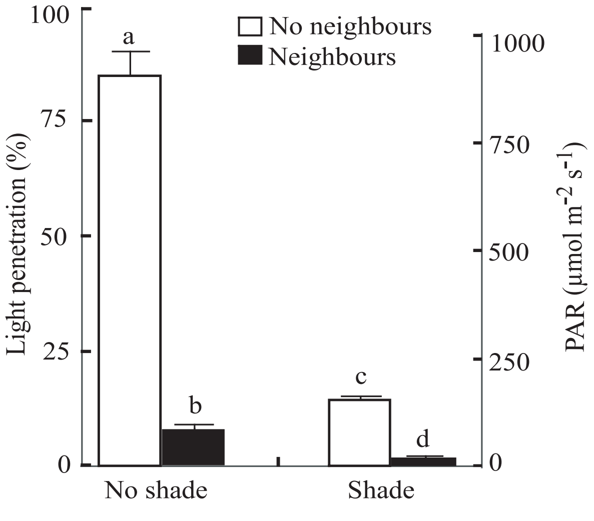
A linear mixed-effects split-split-plot model with residual maximum likelihood estimation (REML, Venables and Ripley 2002) was used to analyze the fixed effects of shade, neighbours and clipping on means of BC. Response variable (BC + 1) was log transformed to reduce heteroscedasticity. Block was included as a random factor, shade as whole plot factor, neighbours as split plot factor and clipping as split-split plot factor. CG response was analysed using REML as described for BC, with species as split-split plot factor. The responses of RNE_Survival and RNE_Growth were analysed using REML with species, shade and clipping as fixed effects, block as a random factor and shade as a whole plot factor.

5.3 Results

5.3.1 Abiotic factors and herbaceous neighbours

Herbaceous neighbours (N^+) reduced light availability to a greater extent than shade (S^+) with the greatest reduction being when neighbours and shade were present (Fig. 5.1). Light penetration was significantly different in each shade x neighbour combination ($\chi^2 = 43$, d.f. 3, $P < .0001$). Air and soil temperature were both significantly reduced by shading and neighbours induced an additionally negative effect on soil temperature (Fig. 5.2; air temp: $\chi^2 = 31$, d.f. 3, $P < .0001$; soil temp: $\chi^2 = 104$, d.f. 3, $P < .0001$). Shade and neighbours also increased air humidity (Fig. 5.2; $\chi^2 = 145$, d.f. 3, $P < .0001$). Surface soil moisture was significantly higher under $S^+ N^+$ conditions (Fig. 5.2; $\chi^2 = 8.6$, d.f. 3, $P < .05$). Shade reduced aboveground biomass production of the neighbouring vegetation significantly ($n = 24$, F = 9.9, d.f. 1, $P < .01$) from a mean (± 1 SE) of 165 ± 10 g m^{-2} in S^- plots to 127 ± 6 g m^{-2} in S^+ plots (a reduction of 24%).

Figure 5.1 Impact of shading and neighbour removal on light environment experienced by saplings. Presented are means (± 1 SE, $n = 48$) of light penetration and photosynthetically active radiation at ground level (PAR) in each combination of the two treatments: shade and neighbours. Data were tested with a Kruskal-Wallis test, followed by Mann-Whitney *U*-tests. Different letters indicate statistically different values ($P < .05$).



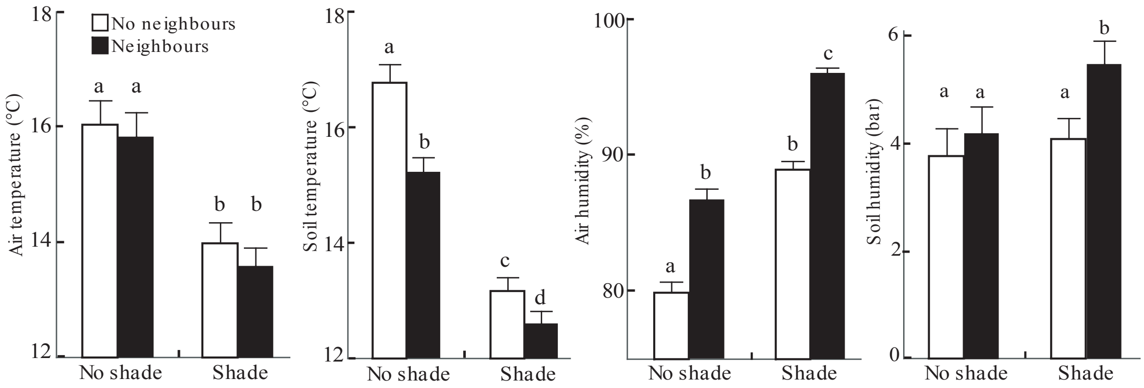


Figure 5.2 Effects of neighbours removal and shade treatments on abiotic conditions experienced by saplings. Presented are means (± 1 SE) of abiotic conditions in each shade x neighbour combination. Data for soil humidity were collected in the growing season of 2004; data of other variables were collected during growing seasons of 2004 and 2005. Data were tested with a Kruskal-Wallis test for each abiotic factor, followed by Mann-Whitney *U*-tests. Different letters indicate statistically different values ($P < .05$).

5.3.2 Survival

Vole predation was a more important cause of death for deciduous than for evergreen saplings with respectively 11% and 5 % mortality. A significantly lower proportion of *Picea* but higher proportion of *Fagus* saplings died due to predation when surrounding vegetation was mown (cause x neighbours: *Picea*: $\chi^2 = 4.9$, d.f. 1, $P < .05$; *Fagus*: $\chi^2 = 8.1$, d.f. 1, $P < .01$). For *Acer* mortality, predation was relatively more important for the unclipped saplings than for the clipped ones (cause x clipping: $\chi^2 = 7.6$, d.f. 1, $P < .01$).

After excluding saplings that died due to predation, mean survival (% ± 1 SE) was 64 ± 5.8 for *Picea*, 78 ± 3.9 for *Acer*, 77 ± 3.7 for *Fagus* and 89 ± 2.6 for *Abies* (Fig. 5.3). Clipping reduced *Picea*, *Acer*, *Fagus* and *Abies* survival by 20 %, 25 %, 5 % and 2 % respectively. These reductions were significant for *Picea* saplings in all cases and *Acer* saplings under S^+ (shade x clipping interaction, Table 5.2, Fig 5.3). Survival was reduced by presence of neighbours for *Picea*, *Acer*, *Fagus* and *Abies* by 44 %, 9 %, 19 % and 5 % respectively. Furthermore, *Picea* and *Acer* sapling survival was positively affected by neighbour removal when shading was present (shade x neighbour interaction, Table 5.2, Fig. 5.3).

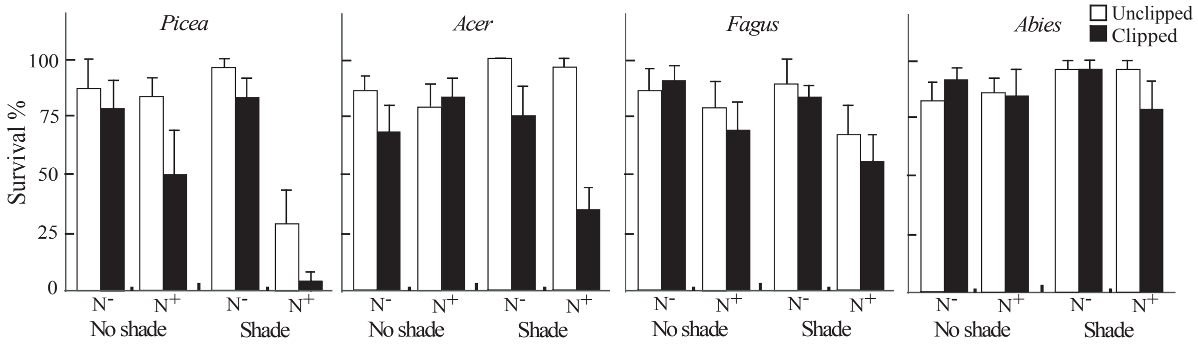


Figure 5.3 Effects of simulated browsing (unclipped and clipped), shading and absence (N^-) or presence (N^+) of neighbours on the survival (%) of saplings of four tree species. Data presented are means (± 1 SE, $n = 6$ per treatment).

Table 5.2 Results of logistic regression, using GLM and chi-squared likelihood ratios for the effects of shade, neighbours and clipping and their interactions on the survival of saplings of four tree species (*n* = 48). Saplings that died due to vole predation were excluded from the analysis.

		Picea		*Acer*		*Fagus*		*Abies*	
	df	χ^2		χ^2		χ^2		χ^2	
shade	1	9.1	**	0.26	ns	0.9	ns	1.0	ns
neighbours	1	45.9	****	2.1	ns	8.9	**	1.0	ns
clip	1	9.8	**	15.8	****	2.7	ns	0.3	ns
shade x neigh	1	14.8	****	6.7	**	0.6	ns	1.4	ns
shade x clip	1	0.5	ns	10.1	**	0.1	ns	2.9	ns
neigh x clip	1	0.8	ns	1.7	ns	0.1	ns	1.4	ns
sh x neigh x cl	1	0.1	ns	0.1	ns	0.1	ns	0.17	ns

P < .05*; *P* < .01**; *P* < .001***; *P* < .0001****; ns: non significant result

5.3.3 Biomass change

Overall, BC of *Picea*, *Acer*, *Fagus* and *Abies* was reduced by the presence of neighbours by 60 %, 56 %, 40 % and 28 % respectively (Fig. 5.4). This positive effect of mowing (N^-) was stronger for unclipped saplings than for clipped saplings (neighbour x clipping interaction, Table 5.3). The negative effect of neighbours was also enhanced by shading, with the exception of *Picea*. Shade increased sapling growth in N^- plots but had a neutral or decreased effect in N^+ plots (shade x neighbour interaction). For *Picea*, the effect of shade was not significant. For *Acer*, differences between clipped and unclipped saplings were larger under shade with a remarkably large increase in the unclipped saplings in S^+N^- plots (shade x clipping interaction, Table 5.3, Fig. 5.4).

Only one compensation event ($CG \geq 1$) was found namely for *Picea* but only is based on *n* = 1 (Fig. 5.5). For all species, CG response was lower in N^+ plots ($F_{\text{neighbour}} = 27.5$, d.f. 1,10, $P < .001$) and differences tended to be larger under S^+ ($F_{\text{shade x neighbour}} = 4.28$, d.f. 1,10, $P < .1$). *Picea* (0.51) had lower mean CG response than *Acer* (0.66), *Fagus* (0.69) and *Abies* (0.70) ($F_{\text{species}} = 3.1$, d.f. 3, 52, $P < .05$) (Fig. 5.5).

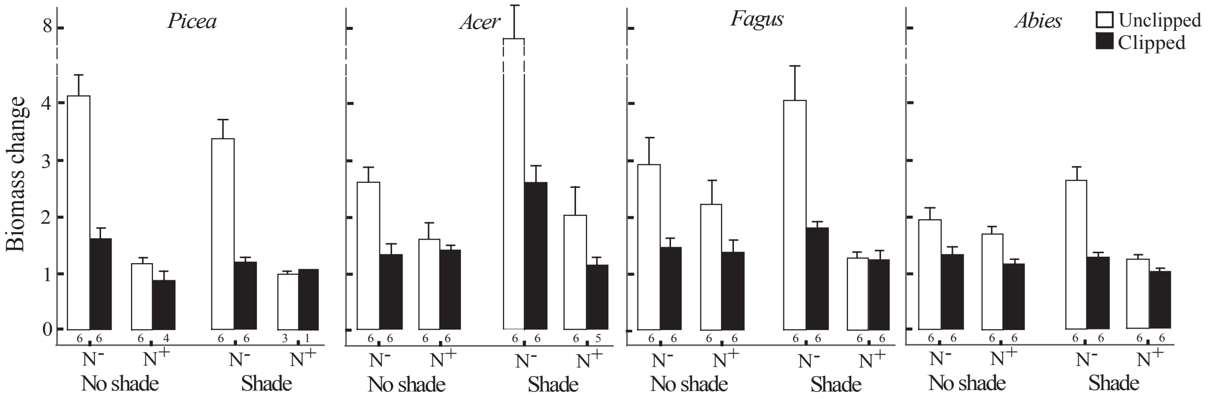


Figure 5.4 Effects of simulated browsing (unclipped and clipped), shading and absence (N^-) or presence (N^+) of neighbours on the biomass change (BC) of saplings of four tree species. Data presented are means (± 1 SE, *n* = 6 per treatment; exceptions are noted). Dead saplings are not included.

Table 5.3 Results of the linear mixed-effects split-plot models with residual maximum likelihood estimation (REML) for the effects of shade, neighbours, clipping and their interactions on biomass change (BC) for saplings of four tree species.

	Picea			*Acer*			*Fagus*			*Abies*		
	n = 38			*n* = 47			*n* = 48			*n* = 48		
shade	$F_{1,5}$	0.09	ns	$F_{1,5}$	24.2	**	$F_{1,5}$	0.02	ns	$F_{1,5}$	0.18	ns
neighbours	$F_{1,7}$	123	****	$F_{1,10}$	42.7	***	$F_{1,10}$	29.5	***	$F_{1,10}$	23.5	***
clip	$F_{1,13}$	106	****	$F_{1,19}$	33.9	****	$F_{1,20}$	31.9	****	$F_{1,20}$	58.0	****
sh x neigh	$F_{1,7}$	0.27	ns	$F_{1,10}$	20.9	**	$F_{1,10}$	10.4	**	$F_{1,10}$	8.38	*
sh x clip	$F_{1,13}$	1.37	ns	$F_{1,19}$	6.14	*	$F_{1,20}$	0.41	ns	$F_{1,20}$	0.79	ns
neigh x clip	$F_{1,13}$	33.8	***	$F_{1,19}$	12.3	**	$F_{1,20}$	9.25	**	$F_{1,20}$	7.60	*
sh x neigh x cl	$F_{1,13}$	0.53	ns	$F_{1,19}$	0.47	ns	$F_{1,20}$	2.25	ns	$F_{1,20}$	7.75	*

$P < .05$*; $P < .01$**; $P < .001$***; $P < .0001$****; ns: non significant result

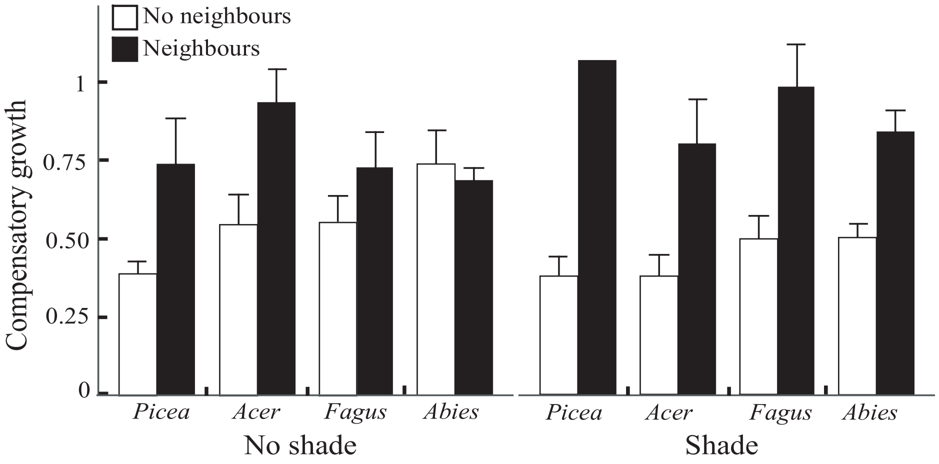


Figure 5.5 Effects of neighbours removal and shade treatments on compensatory growth responses (CG) of saplings of four tree species. Data presented are means (± 1 SE, *n* as in Fig. 5.4). CG was calculated as: (BC_clipped saplings)/(BC_unclipped saplings) (CG >1: overcompensation; CG = 1: compensation; CG < 1: undercompensation).

5.3.4 Relative neighbourhood effect

RNE_Survival was significantly different among species in S^+ plots (species x shade interaction) and between unclipped and clipped saplings (Table 5.4, Fig. 5.6 a). RNE_Growth was significantly higher for unclipped saplings, under shade and differed between species (Table 5.4, Fig. 5.6 b). The negative impact of neighbours on sapling perfomance was greatest for *Picea* saplings; this difference being greatest when saplings were shaded. A facilitative effect was observed for clipped *Acer* saplings and unclipped *Abies* saplings under light. Ranking of the clipped saplings in competition intensity for survival was the same as for growth whereas for unclipped saplings only *Picea* was severely negatively influenced by neighbours under shade.

Table 5.4 Results of the linear mixed-effects split-plot models (REML) for the effects of species, shade and clipping and their interactions on RNE-survival and RNE-growth (*n* = 96).

	RNE_Survival *n* = 96			RNE_Growth *n* = 85		
shade	$F_{1,5}$	15.4	*	$F_{1,5}$	18.9	**
clip	$F_{1,70}$	5.18	*	$F_{1,59}$	25.5	****
species	$F_{3,70}$	7.15	***	$F_{3,59}$	6.62	***
shade x clip	$F_{1,70}$	1.35	ns	$F_{1,59}$	0.21	ns
shade x spec	$F_{3,70}$	3.18	*	$F_{3,59}$	2.36	ms
clip x spec	$F_{3,70}$	0.19	ns	$F_{3,59}$	1.08	ns
sh x cl x sp	$F_{3,70}$	1.63	ns	$F_{3,59}$	1.74	ns

P < .05*; *P* < .01**; *P* < .001***; *P* < .0001****; ms: .05 < *P* < .1; ns: non significant result

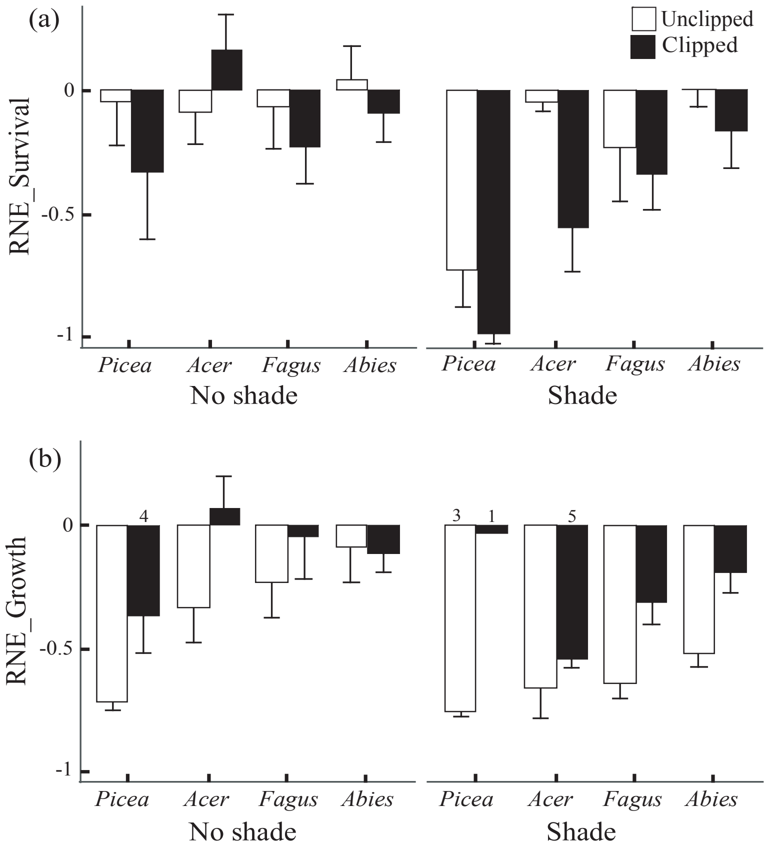


Figure 5.6 Effects of simulated browsing (unclipped and clipped) and shading treatments on the relative neighbourhood effect (RNE) for (a) survival and (b) growth (BC) of saplings of four tree species. Data presented are means (± 1 SE, *n* = 6 per treatment; exceptions are noted). Values range between -1 (competition) and +1 (facilitation).

5.4 Discussion

5.4.1 Competition tolerance

The negative effect of herbaceous neighbours on the performance of the saplings was enhanced under shade. Herbaceous neighbours reduced light availability more than did shade nets, making light a highly contested resource under the combination of both treatments (S^+N^+). Overgrowth by neighbours implied not only a light reduction but likely also an important decrease in space (Husheer *et al*. 2006) and nutrient availability (Wilson 1998; Thevathasan *et al*. 2000). *Picea* was the least competition tolerant tree species (Pagès *et al*. 2003; Heuze et al. 2005) and the effect of competition from neighbours was greater than any direct negative effect of tissue removal per se as found by Prach *et al*. (1996). The competitive hierarchy did change only slightly in response to clipping or shade, contrarily to study of Tripler *et al*. (2005). Competition intensity effects of neighbours on survival were more heavily increased when shade was added for *Picea* and *Acer*. Moreover, the severe competition effect on clipped *Acer* saplings switched under full light into a facilitative effect. *Acer* might be the only species with the growth strategy to respond quickly to favourable shade and moisture conditions provided by neighbours under dry conditions (Gill and Marks 1991).

5.4.2 Browsing tolerance

There were no significant compensation events (sensu Belsky 1993) observed, even for the deciduous species which are considered to have a more flexible growth pattern (Millard *et al*. 2001; Ayres *et al*. 2004; Hester *et al*. 2004). This might be partly due to the fact that summer browsing has more severe consequences than winter browsing (Canham *et al.* 1994; Relva and Sancholuz 2000; Harmer 2001) or due to a delayed growth response (Haukioja and Koricheva 2000). However, Ammer (1996) did not find compensation events either after ungulate winter browsing for the same species. Clipping reduced survival of *Picea* and *Acer* relatively more than for *Abies* and *Fagus* which might be linked to their lower competition tolerance especially in interaction with shade. Although *Acer* persisted less with reduced biomass than *Fagus* as found by Harmer (2001), both deciduous species had similar compensatory growth responses. *Abies* clipping tolerance was surprisingly higher than expected (Ammer 1996; Ayres *et al*. 2004). Impacts of browsing on silver fir sapling performance has hardly directly been measured and the frequent observed failure of fir regeneration is probably more related to higher off-take rate by herbivores or inter-tree competition at later stages than lower sapling browsing tolerance compared to *Picea* (Senn and Suter 2003; Heuze *et al*. 2005).

5.4.3 Shade tolerance

In contrast with the study of Pagès *et al*. (2003), shade increased growth of *Abies*, *Acer* and *Fagus* saplings when surrounding vegetation was mown. One mechanism explaining this could be reduced photoinhibition. Strong irradiance, as found in open pastures, can lead to a decline in photosynthetic efficiency, especially for shade-tolerant species, due to damage of the photosynthetic apparatus (Long *et al.* 1994; Kitao *et al*. 2000; Alves *et al*. 2002; Valladares *et al*. 2002). Light availability in the shaded and mown plots (S^+N^-) corresponded approximately with large forest gaps of 250 m^2 (in Sipe and Bazzaz 1995) and might be considered not to be a limited resource for sapling growth. Furthermore, increased air humidity and reduced temperature conditions under shade will have reduced rates of transpiration. As a result plants are likely to have maintained a larger stomatal aperture resulting in enhanced photosynthetic rates (Holmgren 2000). The maximal growth of *Picea* in full light plots without neighbours (S^-N^-) might be due to their more efficient photoprotective system (McKinnon and Mitchell 2003) and confirm its moderate shade tolerance (Breziecki and Kienast 1994). A second mechanism whereby shade could have facilitated growth in plots without neighbours was by indirect facilitation (Levine 1999; Siemann and Rogers 2003). Under shade, competition for growth with herbaceous vegetation was reduced with about 24 % which could have been enough to reduce belowground competition and enhance nitrogen availability. It was suggested by Pagès *et al*. (2003) that shade-intolerant conservative tree species as *Picea* are poor candidates for positive indirect interactions. Conversely, *Acer* has the essential traits for indirect facilitation, in its ability to respond quickly to increased nutrient availability. Both mechanisms might explain the remarkable increase in biomass of unclipped *Acer* saplings in the shaded mown plots.

5.4.4 Browsing – environmental interactions

Shade, which represented a low stress situation (*i.e*. high BC) for *Acer*, increased the negative effect of clipping on *Acer* survival and growth. Furthermore, simulated browsing stress resulted in relatively smaller growth losses when plants were growing slowly due to competitive conditions. For all species, compensatory growth responses and thus tolerance were higher in presence of neighbours and the differences tended to be larger under shade. Our short-term findings are in contrast with the prediction of the compensatory continuum hypothesis (CCH) that browsing tolerance is reduced under stress (Belsky *et al*. 1993; Mclaren 1996; Weltzin *et al*. 1998; Blundell and Peart 2001; references in Husheer *et al*. 2006). They support however the growth rate model of Hilbert *et al*. (1981) that compensation is more likely to occur under stress. A common explanation given for such phenomenon is that certain stressed plants may actually be more attractive to herbivores as they tend to have higher tissue N and lower concentrations of chemicals (plant stress hypothesis of White 1993), although most evidence comes from insect studies (*e.g*. Ladd and Facelli 2005). The plant-stress hypothesis does not account for clipping experiments. We believe that the increased tolerance under conditions which negatively affected survival and growth is due to the fact that the biomass needed to compensate was smaller as was found for several herbaceous species (Oesterheld and McNaughton 1991; Hicks and Turkington 1999) but also for woody species (Hawkes and Sullivan 2001; Puettmann and Saunders 2001). The degree of tolerance to herbivory was thus not related to plant performance as saplings that compensated almost for clipping damage still had a lower overall growth than less tolerant saplings with high growth rates in both clipped and unclipped states. Furthermore, (over)compensation may be more an adaptation for competitive ability rather than herbivory per se as suggested by several authors (Edenius *et al*. 1993; Hjälten *et al.* 1993; Puettmann and Saunders 2001). A sapling would have thereby concentrated its resources on increasing leader length to over-top potential competitors and increase long-term survival chances.

5.4.5 Ecological implications

Plant resistance to browsing is defined by escape, chemical or physical defence and tolerance (Haukioja and Koricheva 2000; Boege and Marquis 2005). In the wood-pastures of the Swiss Jura Mountains, none of the four co-dominant tree species is avoided by cattle and the probability for the species of being browsed is equal (Vandenberghe *et al*. in press a; Smit *et al*. unpublished data). Repeated browsing events and a varying off-take rate by cattle among species due to different plant architecture, apparancy or chemical composition (Tripler *et al*. 2002; Vandenberghe *et al*. in press) might be expected to cause differences in sapling responses to cattle browsing in natural situations when compared to the outcome of this study. We suggest however that at early sapling life stage, browsing tolerance is linked to tree life history characterises such as shade and competition tolerance. Therefore, browsing may therefore not alter the tree composition dynamics at the early sapling stage but rather accelerate them as proposed by Liang and Seagle (2002). Under situations with intense competitive interactions between neighbours and saplings, *e.g*. no or low grazing intensities (Bakker 1998), the additional stress due to browsing disturbance will have minor effects on saplings performance since smaller growth losses occurred when plants were growing slowly due to competitive conditions. Our results provide an insight into the general expectations of relative importance of browsing, shade and competition tolerance at the early sapling stage.

5.5 Acknowledgements

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Chapter 6

Tree species-specific responses to facilitation by a thorny shrub along a grazing intensity gradient

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and Alexandre Buttler

Abstract

Facilitation of tree regeneration by unpalatable plants against herbivores is a driving mechanism for the dynamics of wood-pastures. Understanding relationships between a nurse plant and saplings of different trees species will permit to improve the management of the endangered wood-pasture ecosystems and maintain the tree species diversity. We experimentally tested the short-term protective effects of planted nurse shrubs (the thorny *Rosa rubiginosa*) on browsing, survival, and growth of saplings of *Abies alba, Picea abies, Acer pseudoplatanus* and *Fagus sylvatica*. These species co-occur in the wood-pastures of the Swiss Jura Mountains. The saplings were planted under and next to (1.5 m) the shrubs, along a grazing intensity gradient (zero, low and high intensity).

Facilitation depended on grazing intensity. Shrubs were more heavily damaged at high intensity than low intensity. Consequently, escaping browsing, sapling survival and biomass was significantly increased by shrubs under low grazing intensity but not under high grazing intensity. Under zero grazing intensity no facilitation effect was detected and survival and growth were higher than in the grazed areas.

Effects of species on sapling survival and growth in interaction with the grazing intensity gradient were found. The survival and growth of *Fagus* was significantly facilitated by shrubs under both low and high grazing intensities. Although the number of saplings browsed did not differ between species, the coniferous species were more sensitive to cattle grazing, *i.e.* they showed higher mortality and biomass decrease than deciduous species. Coniferous species and in particular *Picea* were more favoured by protective shrubs under low grazing intensity than deciduous species. Deciduous species were more favoured by the shrubs under high grazing intensity than coniferous ones, especially during the first grazing periods.

The importance of the positive effects of shrubs differed between species. Therefore, tree species composition dynamics in wood-pastures might be affected by the presence of shrubs. The decreasing grazing intensity in the Jura wood-pastures could have lead to increased tree establishment, in particular for *Picea*. Ancient management practices such as cutting thorny shrubs could be reintroduced to limit facilitation and to prevent tree establishment.

Keywords: associational resistance, positive interactions, nurse shrubs, wood-pastures, planted saplings, secondary succession

6.1 Introduction

Ecological conditions that drive tree establishment in open old-fields or pastures are multi-factorial. Establishment of trees depends on distance of parents and life-history traits, *e.g.* seed production, seed dispersal ability, growth rate and life expectancy of pioneers and late successional species. Furthermore, many abiotic (*e.g.* light, nutrients and water) and biotic factors (*e.g.* seed predation, competition versus facilitation by neighbours, diseases and herbivory) are strong determinants of tree dynamics (Chambers 2001; Smit 2002; Vandenberghe *et al.* 2006b), especially during the early life stages of a tree. Escape (*e.g.* by size, apparency, neighbourhood), defence (*e.g.* by secondary metabolites, spines, thorns), and tolerance (*e.g.* by compensatory growth) are the main mechanisms by which plants can survive and grow in grazed systems.

While negative interactions (*e.g.* concurrence, predation and parasitism) were intensely studied, many examples of positive interactions (facilitation, commensalism) were reported recently determining ecosystem functioning and dynamics, structuring plant communities, and also increasing biodiversity (Bertness and Callaway 1994; Bruno *et al.* 2003; Callaway 1995; Connell and Slatyer 1977; Hacker and Gaines 1997; Olff and Ritchie 1998; Tewksbury and Lloyd 2001; Tirado and Pugnaire 2005; Michalet *et al*. 2006). Positive interactions appear when a neighbouring plant modifies, directly or indirectly, the abiotic or biotic environment and consequently increases the performance of a nearby target plant (protégé) (Bertness and Callaway 1994; Hacker and Gaines 1997; Brooker and Callaghan 1998; Levine 1999). It is considered that negative interactions between species mainly occur when resources (light, nutrients and water) are available such as in mesic, productive sites, whereas positive interactions mainly occur when resources are limited such as in more physically stressed environments (Callaway *et al*. 2002).

Most studies concerning facilitation were realised in stressed, severe abiotic environments, *e.g.* saline (Callaway 1994), arid (Flores and Jurado 2003), or cold (Callaway *et al.* 2002; Choler *et al.* 2001; Kikvidze *et al.* 2005). However, positive interactions might also occur in mesic environments under a biotic stress such as herbivory. In ecosystems driven by large herbivores, unattractive, toxic or thorny plants were found to have a positive indirect effect on palatable herbs, shrubs or trees, *i.e.* associational resistance (Atsatt and Odowd 1976; Milchunas and Noy-Meir 2002). Recent studies showed associational resistance of tree species mediated by unpalatable nurse shrubs (Bakker *et al.* 2004; Meiners and Gorchov 1998; Rousset and Lepart 1999, 2000; Smit *et al.* 2005; Smit *et al.* 2006). Furthermore, Brooker *et al.* (2006) and Smit *et al.* (unpublished data b) found a hump-backed relationship between a biotic stress gradient (herbivory) and facilitation of saplings. Gomez-Aparicio *et al*. (2004) and Gomez-Aparicio *et al*. (2005) demonstrated that the microhabitat, *i.e.* different conditions of abiotic stress (light, soil compaction, water content and soil fertility) created by several nurse shrubs in the field could lead to species-specific responses of transplanted saplings underneath. Facilitative effects of shrubs on different tree species growing in a stressful environment (*e.g.* biotic stress by herbivores) were to our knowledge never investigated.

In pastured systems, the probability of a sapling to be browsed and die after repeated browsing depends on the apparency of the saplings (Vandenberghe *et al.* 2006a), on mechanical defences (*e.g.* stiff and tough needles) or chemical attractive or repulsive compounds and on the specific intrinsic abilities to survive and regrow after repeated browsing (Hester *et al.* 2004; Hester *et al.* 2006). Hence, we might expect that the facilitative effects of a nurse shrub on trees vary between species and among grazing intensities, leading to different tree species composition in a system. We tested experimentally the species-specific relationships to facilitation of four tree species. Two coniferous (*Abies alba* and *Picea abies*) (nomenclature following Lauber and Wagner 2000) and two deciduous tree species (*Acer pseudoplatanus* and *Fagus sylvatica*) were transplanted under and outside the canopy of the thorny shrub *Rosa rubiginosa* in pastures with variable grazing intensities (zero, low and high). All species co-occur naturally in wood-pastures of the Swiss Jura Mountains.

6.2 Methods & Materials

6.2.1 Study area

The experiment was conducted in 2004-2005 in the Swiss Jura Mountains, at ‘La Petite Ronde’ (Les Verrières, 6° 27’ 35’’ E, 46° 56’ 18’’ N, altitude 1125 m a.s.l.). The pasture is low productive, not fertilized, and divided in 3 sites, each containing 3 adjacent paddocks with different grazing intensities due to different paddock sizes (Appendix 1). Each year, cattle graze between May and September following a rotational system with three herds, one of each being attributed to each grazing pressure. In 2004, the herds of 24 two-years-old heifers of different breeds arrived mid May and left the pasture after four rotations of about 30 days (*ca.* 10 days per paddock) at the beginning of October.

The climate in La Petite Ronde is cold and rainy. Yearly mean temperature (± 1 SD) between 1991 and 2003 was 6.7 °C (± 0.67) and yearly mean precipitation (± 1 SD) was 1646 mm (± 424), from which ca. 20 % of snow. Mean monthly temperature and total precipitation during the grazing season (May-September) between 1991 and 2003 were 12.6 °C (± 1.32) and 755 mm (± 126) respectively. The soils are on Argovian marls (Mühlethaler 1930), rich in clay (30 %), acidic ($5.5 < pH < 6.0$), locally hydromorphic, and belong to the brown-soil class (Neyroud 1993).

The sward type is characteristic of pastures of low and mid altitudes in Switzerland (*Cynosurion*) (Delarze et al. 1998). The most frequent (> 90 %) herbaceous species were *Agrostis capillaris, Trifolium pratense, Trifolium repens, Alchemilla xanthochlora* aggr., *Centaurea jacea, Plantago lanceolota, Ranunculus acris* ssp. *friesianus, Festuca rubra* aggr., *Prunella vulgaris*, and *Veronica chamaedrys* (nomenclature following Lauber and Wagner (2000)). Locally some hygrophilous species (*e.g. Juncus* and *Carex*) were present but scattered in the sward.

6.2.2 Experimental design

We used the 3 replicated sites (Appendix 6), each containing 2 paddocks of different sizes (small paddocks 3.71 ± 0.35 (SD) ha and large paddocks 7.42 ± 0.69 (SD) ha) and grazing intensities (low = 94.9 LU days x ha^{-1} and high = 191.8 LU days x ha^{-1}) (Smit et al. unpublished data b). The total cumulative differences (mean ± 1 SE) of sward heights measured before and after four rotations correlated well with grazing intensities (low = 56.7 ± 6.4 mm and high = 90.1 ± 10.7 mm) (Smit et al. unpublished data b). In April 2004, 5 blocks (10 m x 10 m) were evenly distributed in each of the 6 paddocks. In each block, four multi-stemmed thorny shrubs of *Rosa rubiginosa* (1.5 m in height) were transplanted at a distance of 7 m. Transplantation modified weakly the field layer density. Each tree species (*Abies alba, Picea abies, Acer pseudoplatanus*, and *Fagus sylvatica*) was attributed separately to one shrub. Four saplings were planted near a shrub at < 0.1 m from the stem of the shrub (position in) and four were planted at 1.5 m (position out), all according to the cardinal directions (N, E, S, W). Five additional blocks were placed in exclosures at the border of each paddock. In total, 1920 young saplings (1 to 3 years old, Table 6.1) were transplanted *i.e.* 3 sites x 2 grazing intensities x 2 exclosures (yes and no) x 5 blocks x 4 species x 2 positions x 4 saplings. Saplings were obtained from a local nursery (Lobsigen, region of Bern, Switzerland). Prior to plantations of the saplings in the field, we measured heights and diameters (at 1 cm above the root collar) (Table 6.1), and we randomised the saplings. Sapling height was chosen to mimic surviving plants, growing and competing within the field layer but not yet emerging above the herb canopy to be apparent for livestock. Forty extra saplings per species, randomly selected, were cut 1 cm above root collar and measured in height; their aboveground biomass was oven-dried, weighed, and an allometric regression model was used to estimate the initial biomass of the transplanted saplings for each species (Table 6.1).

Table 6.1 Age, initial height (h), diameter (d) at 1 cm above root collar, and estimated initial aboveground dry mass (DM) of the transplanted saplings (n = 480 per species). Means (± 1 SE) are given for each variable and species. Regression formulas, based on extra-saplings, were used to estimate aboveground dry mass from the height and diameter measures on the four species. For all models n = 40 and P < .0001.

Species	age (y)	height (cm)	diam (cm)	Initial DM (g)	Log(DM)	R^2
Abies	3	11.6 ± 0.1	0.262 ± 0.003	0.61 ± 0.01	$0.5402 \times \log(d^2h) - 0.162$	0.666
Picea	2	12.5 ± 0.2	0.264 ± 0.004	1.04 ± 0.3	$0.7283 \times \log(d^2h) + 0.027$	0.843
Acer	1	15.5 ± 0.2	0.292 ± 0.003	0.26 ± 0.01	$0.9101 \times \log(d^2h) - 0.725$	0.955
Fagus	1	19.1 ± 0.2	0.332 ± 0.004	0.51 ± 0.02	$0.8327 \times \log(d^2h) - 0.593$	0.914

6.2.3 Measurements

After each grazing period, we recorded for each sapling whether it was browsed and whether it was still alive. Saplings without living stem (*i.e.* brown under the bark), as well as saplings that were pulled out by cattle, were scored as dead. Browsing and survival were noted for each tree species in each block as the proportion (0.25, 0.50, 0.75, and 1) of the four individuals browsed and still alive in each position near a shrub. Final measurements were done in May 2005, when saplings were harvested. All living saplings were cut 1 cm above the root collar, oven-dried and weighed. The biomass change ratio (BCR) was calculated as final biomass x initial biomass^{-1}, with BCR > 1 representing an increase in biomass; 0 < BCR < 1 a decrease in biomass; and BCR = 0 dead plants.

Associational resistance was measured as the Relative Neighbour Effect (RNE sensu Marham and Chanway (1996), modified by Callaway *et al.* (2002)). For browsing, RNE was calculated as: (performance without neighbour - performance with neighbour) x highest value^{-1}. For survival and growth, RNE was calculated as: (performance with neighbour - performance without neighbour) x highest value^{-1}. For all three parameters, values could theoretically range between +1 (facilitation) and –1 (inhibition).

6.2.4 Statistical analyses

For all response variables we used mean values per species across the 5 blocks in each site x grazing intensity combination in order to avoid pseudoreplication (hence, $n = 3$). For survival, RNE-survival, BCR, and RNE-BCR, we calculated for zero grazing intensity the means of 2 x 5 exclosed blocks within each site to avoid pseudoreplication and because exclosures did not differ within each site.

Grazing intensity (low, high), position (in, out) and species effects (*Abies, Picea, Acer*, and *Fagus*) on browsing, survival and BCR were analyzed using a three-way split-plot ANOVA with site as random factor, grazing intensity as whole plot factor and position and species as split-plot factors. The same analysis was used with the RNE-variables as responses. Data of survival were arcsin transformed to meet normality. For all ANOVAs, differences between means were tested with Tukey post-hoc tests.

Furthermore, we tested for each species, the differences in BCR of individual saplings still alive at harvest with browsing (browsed, unbrowsed), grazing intensity (low, high) and position (in, out) as explanatory variables (hence, *n* varies). Blocks and sites were not considered. Analyses were conducted using Mann-Whitney-U tests since data were not always normally distributed. We tested for differences in BCR between conifers and deciduous saplings of browsed and unbrowsed saplings using the same test.

All data were analyses with R, version 2.2.0. (R Foundation for statistical computing, 2005) and Statview 5.0.1 (SAS Institute Inc., 1998).

6.3 Results

6.3.1 Browsing

The protecting effect of the shrubs on the browsing of saplings (difference between in and out) was high under the low grazing intensity, but decreased significantly under the high grazing intensity (intensity x position interaction) (Table 6.2, Fig. 6.2). Under low grazing intensity, differences between positions increased more than under high grazing intensity during the experiment (Fig. 6.1). Under high grazing intensity, relatively more saplings of *Picea* and *Abies* were browsed under the shrub than outside, but this effect was reversed after the first and second rotation respectively.

After the first grazing period more conifers were browsed (29.2 %) than broadleaved saplings (14.6 %) (Fig. 6.1). However, these differences were no longer significant at the end of the experiment (Table 6.2). Browsing proportions increased mainly during the second rotation for deciduous saplings (Fig. 6.1). For all four tree species, the probability of being browsed was lowest near the shrubs under the low grazing intensity (Fig. 6.2).

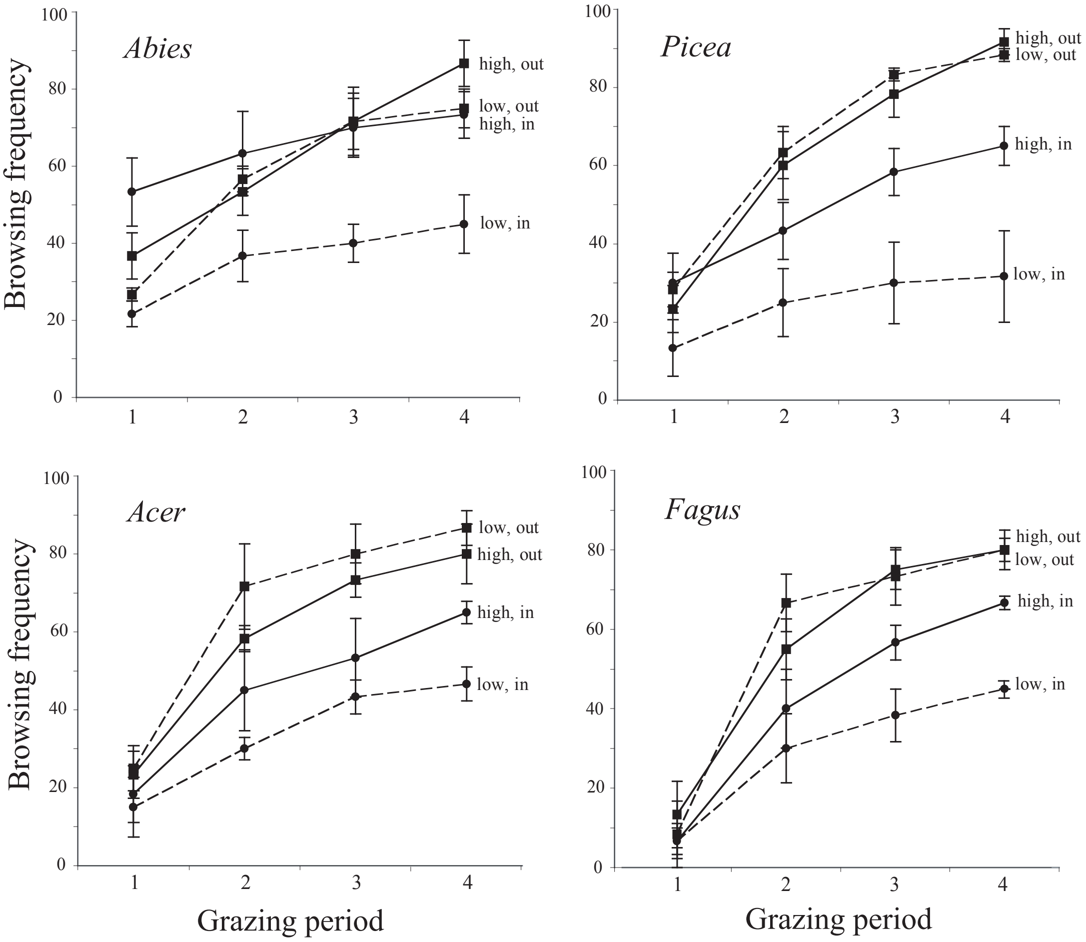

Figure 6.1 Effects of grazing intensity (dashed line: low and solid line: high) and position (in (disks): under the shrub and out (squares): at 1.5 m from the shrub) on the percentage (mean ± 1 SE, *n*=3) of saplings browsed of four tree species, after each of four successive grazing periods during the growing season of 2004 (1 - 4).

Table 6.2 Results of the three-way split-plot ANOVAs with the effects of grazing intensity (whole plot factor), species and position (split-plot factors), and their interactions for a) sapling browsing, b) sapling survival and c) biomass change ratio. Browsing was evaluated after the last rotation; survival and biomass change ratio data were measured at harvest (spring 2005).

a) Browsing			
Intensity	$F_{1,2}$	76.4	*
Species	$F_{3,28}$	0.1	ns
Position	$F_{1,28}$	101.3	***
Species x Intensity	$F_{3,28}$	1.3	ns
Species x Position	$F_{3,28}$	2.4	ns
Intensity x Position	$F_{1,28}$	16.7	***
Species x Intensity x Position	$F_{3,28}$	0.2	ns

b) Survival			
Intensity	$F_{2,4}$	47.7	**
Species	$F_{3,42}$	4.1	*
Position	$F_{1,42}$	24.5	***
Species x Intensity	$F_{6,42}$	5.5	***
Species x Position	$F_{3,42}$	0.7	ns
Intensity x Position	$F_{2,42}$	13.2	***
Species x Intensity x Position	$F_{6,42}$	1	ns

c) Biomass change ratio			
Intensity	$F_{2,4}$	36.4	**
Species	$F_{3,42}$	3.2	*
Position	$F_{1,42}$	56.7	***
Species x Intensity	$F_{6,42}$	2.6	*
Species x Position	$F_{3,42}$	1.7	ns
Intensity x Position	$F_{2,42}$	15.2	***
Species x Intensity x Position	$F_{6, 42}$	0.3	ns

$P < .05$*; $P < .01$**; $P < .001$***; ns: non significant result.

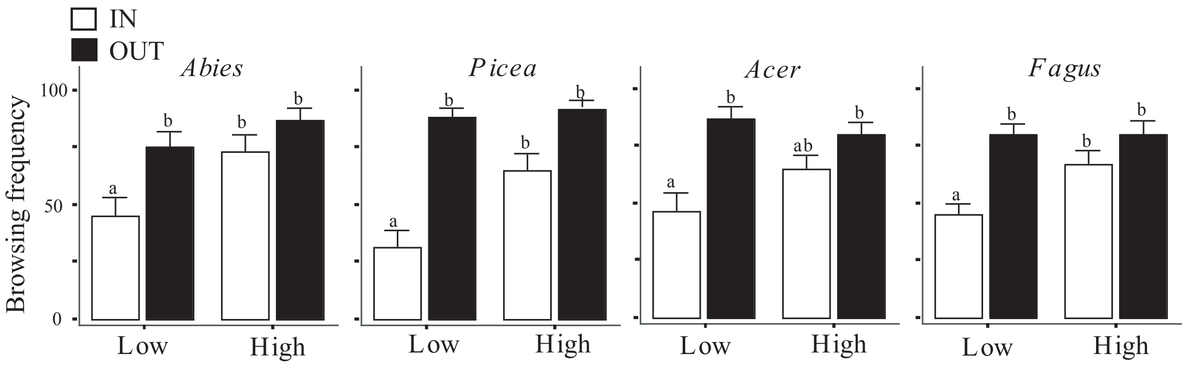

Figure 6.2 Effects of grazing intensity (low and high) and position (white bars = in: under the shrub, and black bars = out: at 1.5 m from the shrub) on the percentage (mean ± 1 SE, *n*=3) of sapling browsed of four tree species after the fourth grazing period. Different letters indicate significantly different means (Tukey post hoc comparisons, $P < .05$)

6.3.2 Survival

The protective effects of the shrubs on sapling survival were significant under low grazing intensity for all species, and under high intensity for *Fagus* (intensity x position interaction, Table 6.2, Fig. 6.4). These effects were high under the low grazing intensity and intermediate under the high grazing intensity. No facilitative effects were found in the absence of cattle. Survival differences between species depended on grazing intensity (species x intensity interaction) (Table 6.2, Fig.6.4). Under grazing, survival of coniferous species was lower than for deciduous ones. Overall survival was 67 %, 68 %, 76 %, 76 % for *Abies, Picea*, *Acer*, and *Fagus* respectively.

During the course of this study sapling survival remained high in the exclosures, but decreased rapidly in the grazed paddocks (Fig. 6.3). The presence of cattle affected coniferous species more rapidly than broadleaved ones. Under high grazing intensity saplings of *Picea* and *Abies* showed a lower survival under shrubs than outside shrubs, but this effect was reversed after winter (Fig. 6.3).

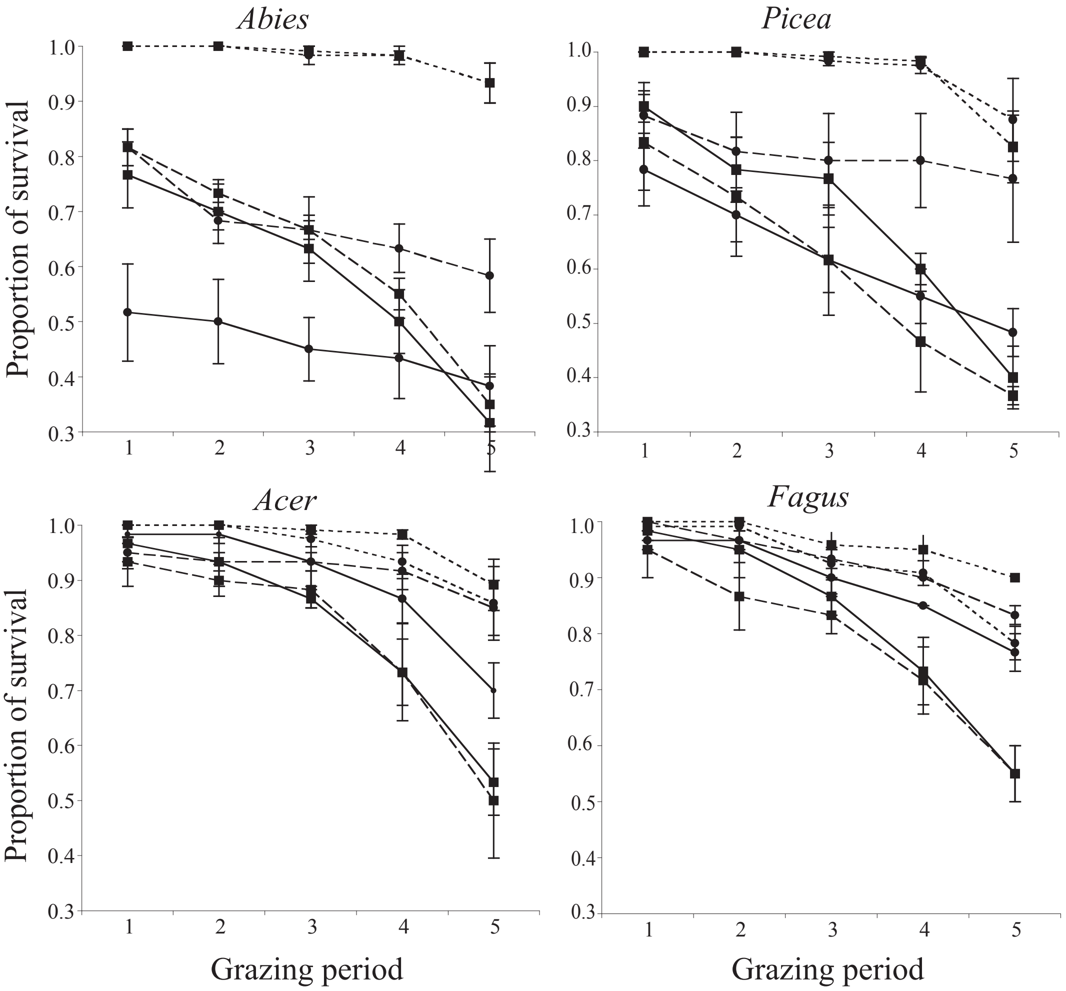

Figure 6.3 Effects of grazing intensity (dotted line: zero, dashed line: low and solid line: high) and position (in (disks): under the shrub and out (squares): at 1.5 m from the shrub) on the proportion (mean ± 1 SE, *n*=3) of survived saplings of four tree species after each of four successive grazing periods during the season 2004 (1 - 4) and after the subsequent winter 2004-2005 (5).

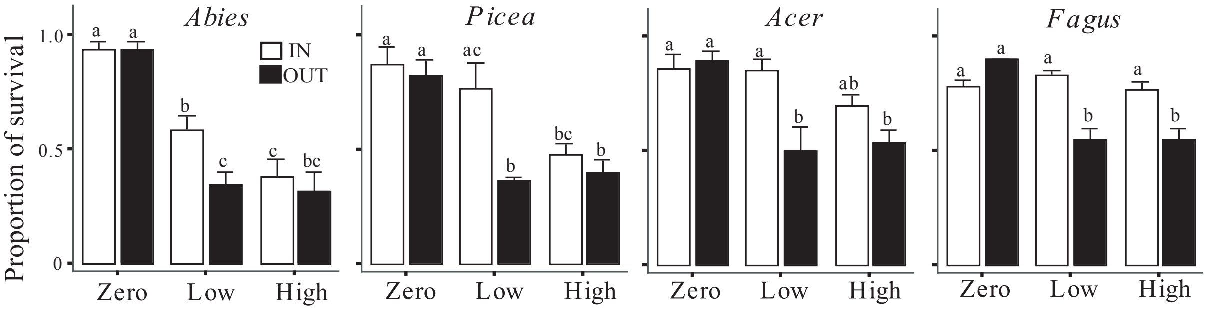

Figure 6.4 Effects of grazing intensity (zero, low, and high) and position (white bars = in: near the shrub, and black bars = out: at 1.5 m from the nurse shrub) on the proportion (mean ± 1 SE, *n*=3) of survived saplings of four tree species at harvest (spring 2005). Different letters indicate significantly different means (Tukey post hoc comparisons, *P* < .05).

6.3.3 Biomass change ratio

The positive effects of the shrubs on the biomass change ratio (BCR) of the saplings were only significant under low grazing intensity (intensity x position interaction, Table 6.2). However, the positive efffect was higher under high grazing intensity than zero intensity. The differences between species depended on the grazing intensity (species x intensity interaction). BCR was higher for deciduous than coniferous species in presence of cattle but not in absence of cattle (Table 6.2, Fig. 6.5).

On average, saplings increased in biomass (6.2 %) near shrubs, but they lost biomass (25.7 %) outside shrubs. Under low and high grazing intensity biomass loss was 21.2 % and 41.6 %, respectively. Saplings in exclosures increased in biomass with 33.5 %.

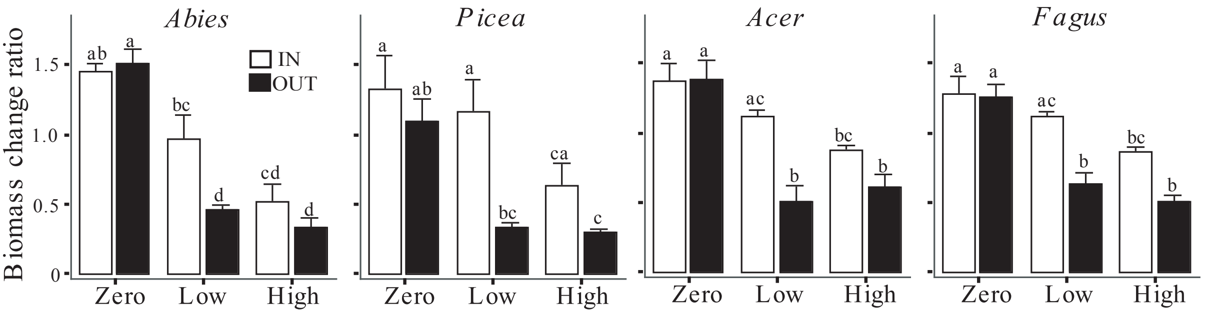

Figure 6.5 Effects of grazing intensity (zero, low and high) and position (white bars = in: near the shrub, and black bars = out: at 1.5 m from the nurse shrub) on biomass change ratio (mean ±1 SE, *n*=3) of four tree species at harvest (spring 2005). Different letters indicate significantly different means (Tukey post hoc comparisons, *P* < .05).

When considering only living saplings the effects of browsing status and position on BCR were significant for all tree species. The effects of grazing intensity on BCR were only significant for *Fagus* and *Picea* (Table 6.3, Fig. 6.6). Unbrowsed coniferous species (mean ± 1 SE, 1.616 ± 0.058) increased significantly more in biomass than unbrowsed deciduous saplings (1.393 ± 0.042) (U= 6842, $P = 0.008$). Contrarily, the browsed conifers (0.803 ± 0.045) decreased significantly more in biomass than the browsed deciduous (1.033 ± 0.033) (U= 4997, $P < .001$).

Table 6.3 Differences in biomass change ratio, measured in the spring 2005, of living saplings pooled in two separated groups according to browsing status (browsed-unbrowsed), position (in-out) and grazing intensity (low-high): results of the Mann-Whitney-U tests. U-values are given for each species and variable.

	Species	*n*	U	
Browsing				
	Abies	98	432	***
	Picea	121	298	***
	Acer	155	1464	***
	Fagus	162	1954	***
Position				
	Abies	98	730	**
	Picea	121	880	***
	Acer	155	2217	*
	Fagus	162	2398	**
Grazing intensity				
	Abies	98	972	ns
	Picea	121	1373	*
	Acer	155	2900	ns
	Fagus	162	2488	**

$P < .05$*; $P < .01$**; $P < .001$***; ns: non significant result.

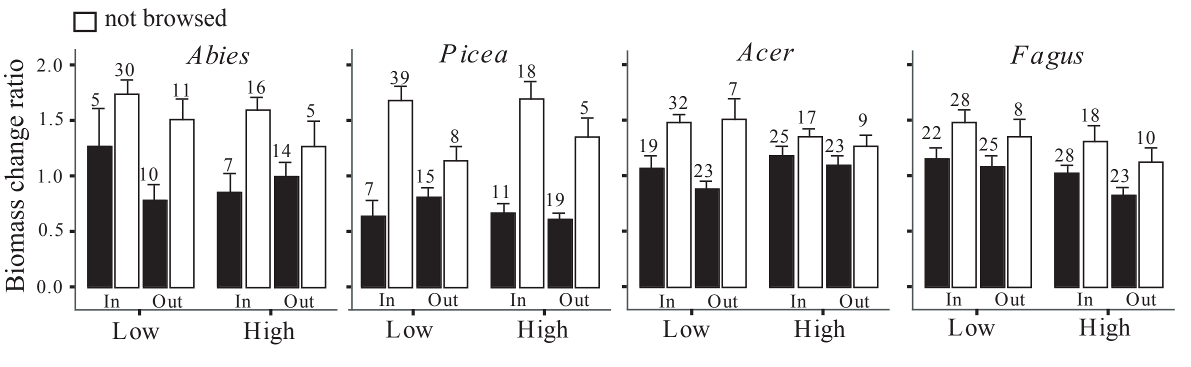

Figure 6.6 Effects of grazing intensities (low and high) position (in: near the shrub, and out: at 1.5 m from the shrub) and browsing status (black bars: browsed, white bars: not browsed) on biomass change ratio of saplings still alive at harvest. Data present means (± 1 SE) and *n* is given for each category (at the top of each bar).

6.3.4 Relative neighbourhood effect

Grazing intensity had a significant effect on RNE-browsing ($F_{1,2} = 62.0$, $P = 0.016$), RNE-survival ($F_{2,4} = 36.2$, $P = 0.003$) and RNE-BCR ($F_{2,4} = 41.7$, $P = 0.002$). No significant effects of species on RNE-browsing were detected (RNE-browsing: $F_{3,12} = 1.63$, $P = 0.24$; RNE-survival: $F_{3,18} = 0.14$, $P = 0.94$; RNE-BCR: $F_{3,18} = 2.30$, $P = 0.11$). However, the positive effects of shrubs tended to be higher for *Picea* (Fig. 6.7). For all response variables and species, except for *Fagus*, facilitation was approximately twice larger under low than under high grazing intensity, although not always significant (Fig. 6.7). Differences in RNE-survival between low and high intensities were only for coniferous species significant. In absence of cattle, shrubs had a small positive effect on survival and BCR for *Picea* whereas for the three other species shrubs had a small negative effect on survival and BCR (Fig. 6.7)

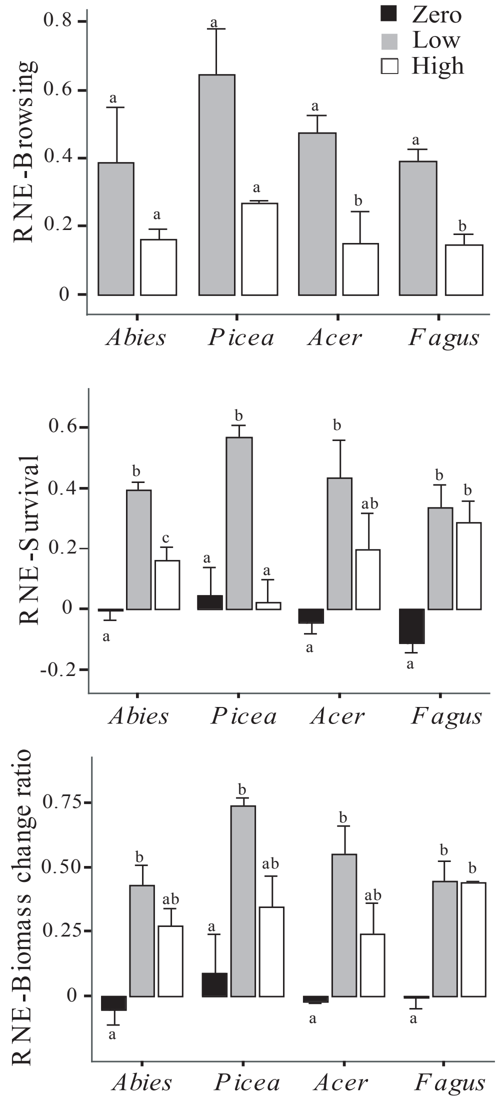

Figure 6.7 Relative neighbour effect (RNE) for browsing frequency, survival and biomass change ratio (end of the experiment, spring 2005), of four tree species under three grazing intensities (zero (black), low (grey) and high (white)). Data presented are means (± 1 SE, *n*=3) and different letters indicate significantly different means per species (Tukey post hoc comparisons, $P < .05$). Values range between -1 (competition) and +1 (facilitation).

6.4 Discussion

6.4.1 Facilitation along a grazing intensity gradient

Strong effects of grazing intensity on the facilitation process between nurse shrubs and saplings were found. Facilitation increased under low grazing intensity but decreased under high grazing intensity and was lowest under zero grazing intensity. Microsites and resources (nutrients, light) of the mesic field layer most likely did not differ sufficiently under and outside the shrub, leading to the lack of facilitation in cattle excluded areas. At the low grazing intensity, the selectivity of patches by cattle was high and led to a good protection from the thorny shrub. Nurse shrubs were significantly more damaged under high intensity (Smit *et al*. unpublished data b) most likely due to a decreased selectivity of cattle (Crawley 1983). This resulted in an enhanced likelihood to be browsed, mortality and biomass loss of saplings near the shrub and thus decreasing facilitation under high grazing intensity. Few examples (Gomez *et al.* 2001) report a greater susceptibility of saplings by browsing near isolated shrubs compared to in open grasslands. Cattle effects on browsing frequency, survival and growth of saplings growing outside the shrub were equal under both low and high grazing intensities.

6.4.2 Species effects

We observed important effects of species on sapling survival and growth, in interaction with the grazing intensity gradient. Mortality and loss of biomass due to cattle browsing were larger for coniferous species. We suppose that a more vulnerable plant architecture resulted in a greater biomass off-take for evergreen saplings. Indeed, the dense and large horizontal branches of coniferous saplings were closer to the canopy of the field layer than the erected and less dense branches, with later leaf expansion, of broadleaved saplings. Additionally, deciduous species could have compensated better for lost biomass due to a greater flexible growth pattern and neoformed growth (Chapin *et al.* 1990; Millard *et al*. 2001; Hester *et al*. 2004). Consequently, the protective effect of shrubs tended to be larger for coniferous species, but only under low grazing intensity where the facilitation process was present. In particular the survival of *Picea* was favoured by facilitation. This might be explained by the low competition tolerance of *Picea* (Pagès *et al*. 2003). Competition from herbaceous neighbours was most likely reduced beneath the shrub and might explain the weak facilitative effect of shrubs for *Picea* in exclosures. No species effect was detected for browsing frequency, in agreement with Vandenberghe *et al.* (2006a). Each of the four species had the same probability of being browsed with the surrounding vegetation.

The temporal pattern of the effect of shrubs on browsing (Fig. 6.1) and survival (Fig. 6.3) differed between coniferous and deciduous species. During the first grazing periods, the coniferous species, mainly *Abies*, were more frequently browsed and showed a higher mortality than the deciduous species. Under high grazing intensity, the shrubs had negative effects on survival and growth for the evergreen species: saplings were more damaged under the shrubs than outside shrubs. The shrubs were apparent and were browsed by cattle, leading to higher browsing and mortality rates of saplings under the shrub. Due to the negative effects of shrubs for evergreen species, facilitation under high grazing intensity tended to be greater for deciduous species, in particular for *Fagus* and during the first grazing periods (Fig. 6.7).

6.4.3 Management implications

Many factors seem to drive facilitation in wood-pasture, *e.g*. type and the efficiency of the nurse plants, site productivity and field layer palatability, mosaics of plant assemblages, landscape roughness, type of livestock, their behaviour and grazing intensities. We showed that the four tree species responded differently to nurse shrubs at a gradient of grazing intensities. This may have effects on tree species composition of the studied wood-pastures. Our results can be used to conserve the typical wood-pasture landscape of the Swiss Jura Mountains.

Maintaining nurse shrubs in xeric habitats permitted to favour secondary succession and was a good ecological and economical alternative to reforestation (Castro *et al.* 2002a; Castro *et al.* 2002b; Castro *et al.* 2004). Land use abandonment increased in the Swiss Jura wooded pastures since the 1950-1970s and led to an extension of forested areas (Gallandat *et al.* 1995). Grazing is needed to conserve the grassland component of wood-pastures. However, we suggest that grazing intensities need to be maintained low, in order to increase frequencies of unpalatable plants such as shrubs, and increase facilitation processes which enhance tree establishment, in particular of *Picea*.

6.5 Acknowledgements

We thank the agronomic research station of Agroscope Changins (RAC) and in particular J. Troxler for providing us the site, material and information about La Petite Ronde. We thank S. Attinger, C. Rosat, L. Freléchoux, M. Köppen and T. Ekamper for field assistance, and M. Burkhard for providing geological data. We acknowledge the support of the National Centre of Competence in Research (NCCR). This study was financially supported by MAVA and the Swiss Federal Research Institute WSL (program Walddynamik).

Chapter 7

Synthesis

7.1 Introduction

I have shown that cattle negatively activity affects tree regeneration in wood-pastures. However, the magnitude of the effect of cattle damage depended on grazing intensity and on other factors such as competition from neighbours, protection by nurse shrubs and surrounding vegetation, tree species, tree size, shading and microclimatic variables. Both competitive (negative) and facilitative (positive) interactions were found between trees and surrounding vegetation which illustrates the complex and potentially transient nature of plant-plant and plant-animal interactions existing in wood-pastures.

In this final chapter, I summarise and combine the major findings of chapters 2 – 6 and study 6 (not presented in foregoing chapters*) in order to come to a synthesis of the importance of cattle activity on tree establishment of four common tree species in wood-pastures. Tree resistance to cattle grazing activity is compared among the seedling, small and large sapling stages and grazing intensities. The two sapling size classes, small and large, are defined by height rather than age (Table 7.1). Grazing intensities are subdivided in low and high, the exact values varying slightly between years and studies (Table 7.2). Besides general observed patterns, the various species-specific responses are discussed.

Table 7.1 Age and initial height (mean ± 1 SE; *n* is given) of small and large saplings of four tree species, at transplantation time of the experiments that started in 2003 (Ch. 4) and 2004 (Ch. 5, Ch. 6 and Study 6).

Plantation exp		2003			2004		
		n	Age	Height (cm)	*n*	Age	Height (cm)
Abies	small	64	3	12.6 ± 0.3	480	3	11.6 ± 0.1
	large	64	6	40.6 ± 0.9	120	5	27.5 ± 0.4
Picea	small	64	2	12.3 ± 0.3	480	2	12.5 ± 0.2
	large	64	5	50.6 ± 1.1	120	4	45.8 ± 0.5
Acer	small	64	1	18.6 ± 0.6	480	1	15.5 ± 0.2
	large	64	3	58.8 ± 1.2	120	3	44.1 ± 0.5
Fagus	small	64	1	16.8 ± 0.5	480	1	19.1 ± 0.2
	large	64	3	57.1 ± 1.1	120	3	51.7 ± 0.7

---

* In study 6, the effect of cattle grazing intensity on survival and growth of large saplings were investigated (Table 7.1). The experiment started in May 2004. Ten blocks of 6 m x 6 m, were randomly placed in each of the 6 paddocks and 6 exclosures (total of 120 blocks or 480 transplanted saplings), used for the experiment described in Chapter 6 (Appendix 6). One sapling of each of the four species was randomly assigned to the corners of each block. Large saplings were monitored after each of the 4 grazing periods of 2004, after the seventh grazing period in 2005 and harvested in May 2006 before the arrival of the cattle.

Table 7.2 Grazing intensities of the years 2003, 2004 and 2005 for the field experiments carried out at ‘La Petite Ronde’. Intensities are calculated as Livestock Units x days x ha^{-1} (LU = 600 kg). The experiment carried out in year 2003 (Ch. 4) was subjected to 3 months of cattle grazing (or 2 grazing periods); the experiments carried out in year 2004 and 2005 (Ch. 3, Ch. 6 and Study 6) were each subjected to 5 months of cattle grazing (or 4 grazing periods).

Grazing intensity	Low	High		
Sowing exp.				
2004	120	198	4 grazing periods	Chapter 3
Plantation exp.				
2003	94	128	2 grazing periods	Chapter 4
2004	95	192	4 grazing periods	Chapter 6 / Study 6
2005	120	227	4 grazing periods	Study 6

7.2 Tree establishment in wood-pastures

7.2.1 Seedling stage

In chapter 3, I showed that seedling establishment decreased with increasing cattle grazing intensity. Direct browsing (biomass off-take), trampling and dunging activities limited seedling emergence and survival. The absence of cattle activity indirectly increased rodent seedling damage effects. Differences in one-year old seedling establishment between ungrazed and cattle grazed areas were never larger than 13 % since other factors than cattle such as competition from neighbours, (micro)climatic conditions and predators (*e.g.* fungi, insects, rodents and birds) also limited establishment in the grassland.

Both facilitative and competitive interactions between surrounding vegetation and tree seeds and seedlings were found (Ch. 2 and Ch. 3). I predict factors other than cattle activity influencing seedling establishment by comparing the emergence, survival and establishment rates of the sowing experiments carried out in (1) 2003 (Ch. 2) and (2) 2004-2005 (Ch. 3) (Fig. 7.1). Emergence was about complete 3 months after sowing. Competitive effects of the surrounding herbaceous vegetation on seedling emergence were found in the very dry and warm year 2003 whereas facilitative effects were found in 2004 when climatic conditions were less stressful. These results are in contrast to the proposition that positive interactions increase under stressful conditions (Bertness and Callaway 1994, Brooker and Callaghan 1998). Competitive effects by neighbours on emergence were likely enhanced under the dry conditions of 2003 (see Michalet 2006). However, an increased seed predation by birds in gaps might also explain the positive effects of neighbours in 2004 (Ch. 3). Seedling survival and establishment were overall lower in 2003 than in 2004 probably due to extreme dry and warm weather conditions that year (Fig. 7.1). The short duration of moist conditions at the soil surface might have been the most critical constraint for seedling survival in 2003 (Farmer 1997). *Picea* survival was even facilitated by the intact vegetation (*i.e.* no gap) likely due to favourable moisture conditions.

The seedling establishment outcome of both experiments was a combination of emergence and survival rates, pointing out the importance to frequently observe seed and seedling fate in order to understand processes influencing the seedling stage. From both Chapters 2 and 3, it might be concluded that the effects of gaps in vegetation, which might be created by cattle, on tree establishment are complex as a result of biotic (predators, competition from neighbours) and abiotic (moisture, light, temperature) interactions and lead to different results in seedling establishment in different years.

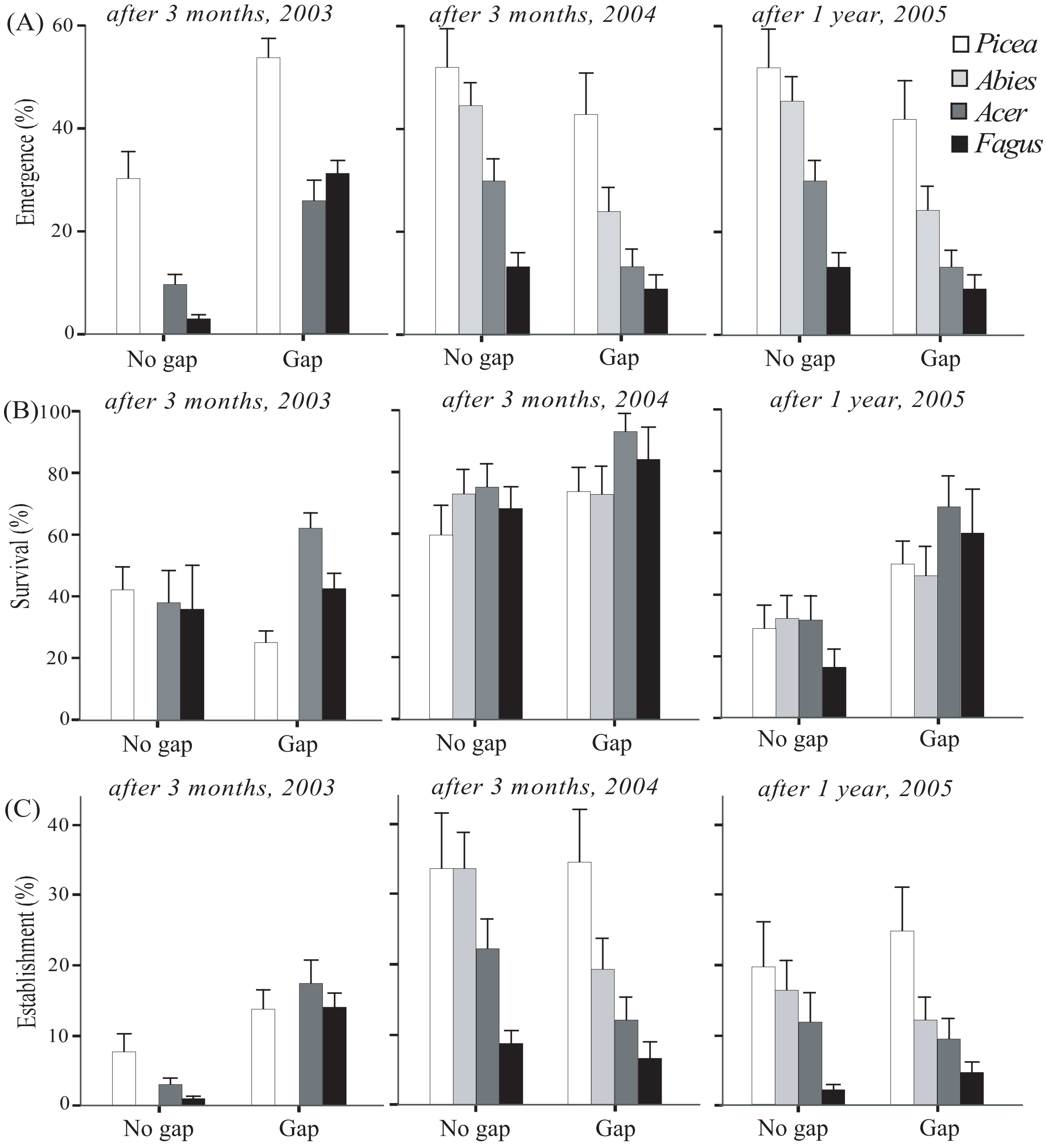

Figure 7.1 (A) Emergence, (B) survival and (C) establishment rates of seedlings from two sowing experiments carried out in (1) 2003 (results 3 months after sowing) and (2) 2004-2005 (results 3 months and 1 year after sowing). Sowing from both experiments took place in May. Data present means (% ± 1 SE) and are corrected for germinability. For experiment 1 (Ch. 2), data of the different sizes of gaps (vegetation was physically removed) were grouped to calculate means of 'gaps'. *Abies* failed to germinate. For experiment 2 (Ch. 3), only data of plots protected from cattle grazing were included to calculate means of 'no gap' and 'gap' (herbicide application).

The interplay of the different factors on seed and seedlings in a pasture resulted in the following species ranking for seedling establishment: *Picea* > *Abies* > *Acer* >> *Fagus* (Fig. 7.1; Ch. 3: Table 3.2). *Fagus* appears less adapted to seedling establishment in pasture environments. Although *Acer* had relative lower emergence rates than coniferous species, it had the largest survival rate, typifying fast-growing pioneer species' establishment in pastures (Aide *et al*. 1996; personal observation). In a dry and warm year, *Picea* and *Abies* will most likely lose this establishment advantage due to high desiccation risks. Furthermore, the reduction in seedling survival due to cattle activity was lowest for *Picea*, intermediate for *Abies* and *Acer* and highest for *Fagus* (Fig. 7.2). Large-sized deciduous seedlings were more vulnerable for direct browsing events than small-sized coniferous species (Ch. 3: Fig. 3.4). The chance of seedlings to survive after being browsed by cattle was low since they did not have enough resource for tolerance (Boege and Marquis 2005). Consequently, the biomass of seedlings still alive at harvest was not affected by cattle.

7.2.2 Small sapling stage

Due to their small size, 25 % and 15 % of the small saplings were able to escape browsing after respectively two and four cattle grazing periods (Fig. 7.3). The chance to escape did not differ between species or grazing intensities (Ch. 4 and Ch. 6). Sapling survival and growth were slightly lower under low grazing intensities but rarely significant (Ch. 4 and Ch. 6). Sapling survival was on average 89 %, 44 % and 45 % under zero, low and high grazing intensity respectively (Fig. 7.2). Sapling survival was lower under real cattle activity than under simulating browsing (*i.e*. clipping) treatment (Ch. 5 versus Ch. 6). This was most likely due to more repeated browsing events and larger amount of biomass removed under real cattle grazing (Canham *et al*. 1994; Hester *et al*. 2004). The aboveground biomass of surviving small saplings was reduced on average with 28 % and 39 % under low and high grazing intensities after 4 grazing periods respectively (Ch. 6).

Coniferous species showed higher mortality rates and higher biomass losses than deciduous species (Ch. 4 and Ch. 6). *Abies* and *Picea* seemed to be submitted to a higher biomass off-take when browsed probably due to a more vulnerable plant architecture. Moreover, deciduous saplings were maybe able to compensate partly for their biomass losses through a greater flexible growth pattern and neoformed growth (Millard *et al*. 2001), although evidence is lacking (Ch. 5).

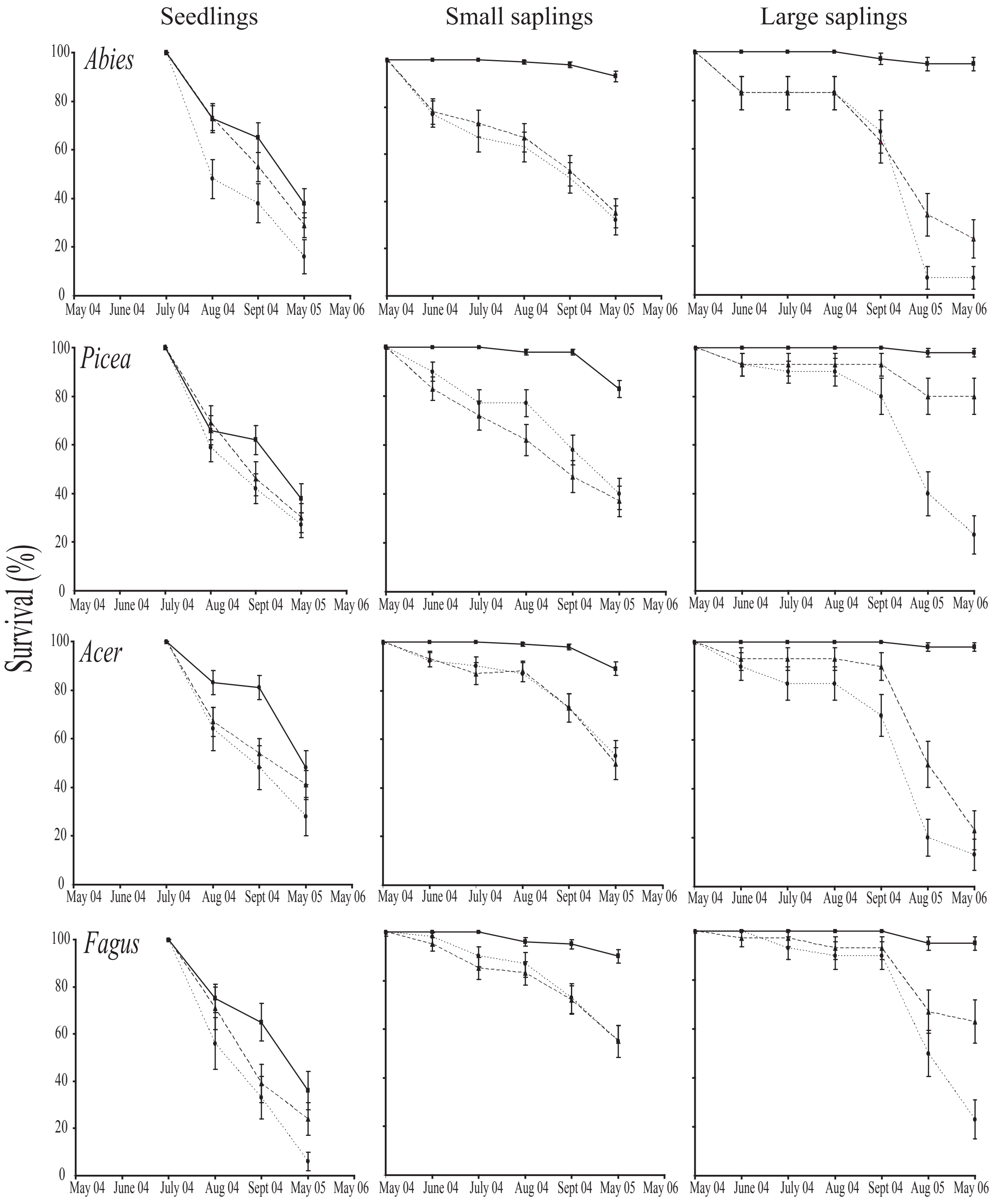

Fig. 7.2 Survival rates (%) for each of the establishment stages: seedling (Ch. 4), small sapling (Ch. 6) and large sapling (Study 6) stage, and for four tree species, under zero (solid line), low (dashed line) and high (dotted line) cattle grazing intensity. Note that the duration between observation dates varies.

As for the seedling stage, both competitive and facilitative interactions between surrounding vegetation and saplings were detected (Ch. 4, Ch. 5 and Ch. 6). It was important to include observations after winter to detect competition effects on survival. Competition from herbaceous neighbours was found to have large negative effects on small sapling performance, which was enhanced by shade. Hence, shade did not indirectly facilitate the performance of the saplings (Ch. 5). From chapters 5 and 6, the following trend in competitive hierarchy for small saplings in pastures was found: *Abies* > *Fagus* > *Acer* >> *Picea*. Although *Picea* was least competition tolerant, it was the only species not negatively affected by strong irradiance as found in an open pasture.

Besides competition, facilitation is another key process driving the dynamics of wood-pastures. In grazed ecosystems, unpalatable plants protect saplings against cattle grazing and consequently enhance tree establishment (Bakker *et al.* 2004; Smit 2005). Recently, Brooker *et al*. (2006) and Smit *et al*. (unpublished data b) investigated the relationship between a biotic stress gradient, *i.e.* grazing disturbance, and facilitation for saplings. They both found a hump-backed relationship, *i.e*. the facilitative effect of the nurse plant was highest at intermediate levels of browsing intensity. In Chapter 6, we demonstrated that for each of the four tree species, performance was highest when protected by thorny shrub species under low grazing intensities. Shrubs were more heavily damaged at high intensity than low intensity. Consequently, escaping browsing, sapling survival and biomass was significantly increased by shrubs under low grazing intensity but not under high grazing intensity. Moreover, species-specific responses to facilitation were found. Under high grazing intensities, the positive effects of shrubs were higher for the survival of the deciduous species, especially during the first grazing periods. On the other hand, under low grazing intensities, the indirect facilitation from shrubs was higher for coniferous species and in particular *Picea* saplings, due to their higher susceptibility towards browsing.

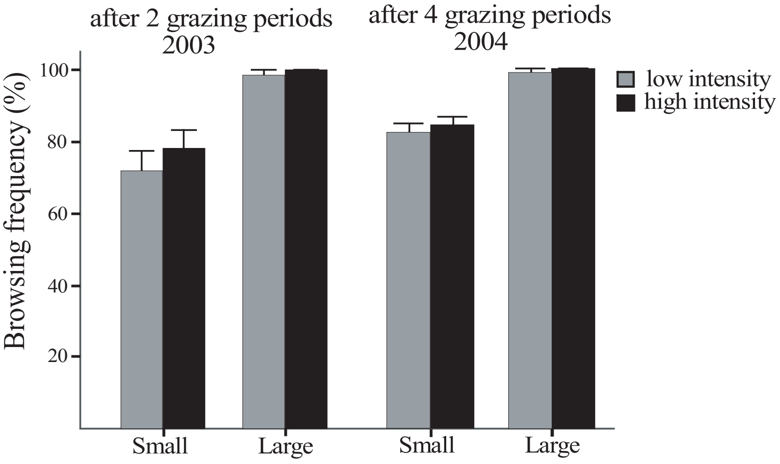

Figure 7.3 Browsing frequency of small and large saplings, under low and high grazing intensity after 2 grazing periods (plantation experiment of 2003, Ch. 4) and 4 grazing periods (plantation experiments of 2004, Ch. 6 and Study 6).

7.2.3 Large sapling stage

Large saplings have a greater apparancy due to their larger size and plant architecture which impeded each of the four species to escape browsing under cattle grazing intensities varying between 95 – 192 Livestock Unit days x ha^{-1} (Fig. 7.3; Ch. 4 and Study 6). Contrary to small saplings, both survival and growth were significantly more negatively affected under high grazing intensities (Study 6; Fig. 7.2). Survival chances were overall 97 %, 47 % and 17 % under zero, low and high grazing intensity respectively (Fig. 7.2). The aboveground biomass of large saplings that survived browsing was reduced on average with 46 % and 65 % under respectively low and high grazing intensities after 8 grazing periods (Study 6). Growth rate in exclosures after two years was lower than expected, probably due to roe deer browsing damage during winter which affected 88 % of the large saplings. Despite high biomass losses, *Picea* (80%) and *Fagus* (63%) had a relatively high survival under low cattle grazing intensity. However, survival for all species under high grazing intensities was never higher than 23 % (Table 7.2).

7.3 Synthesis: Resistance to cattle activity

In accordance with the previous paragraphs, I propose a pattern of changes in resistance to cattle activity during the tree establishment phase of four tree species in wood-pastures (Fig. 7.4). Tree resistance encompasses both avoidance (escape and defence) and tolerance (intrinsic and extrinsic) strategies (Ch. 1). I estimated resistance based on the differences in survival and growth of seedlings and saplings growing in 'cattle exposed' (2 grazing intensities) and 'cattle excluded' areas. However, young trees in 'cattle excluded' areas will be exposed to different hazards and causes of death than in 'cattle exposed' areas. Therefore, resistance as defined here implies the relative importance of cattle activity compared to other limiting factors in cattle excluded areas. Consequently, highly resistant plants might have lower survival and growth chances than less resitant plants. The seed phase is not included in the schema due to lack of precise insight of cattle activity on seeds.

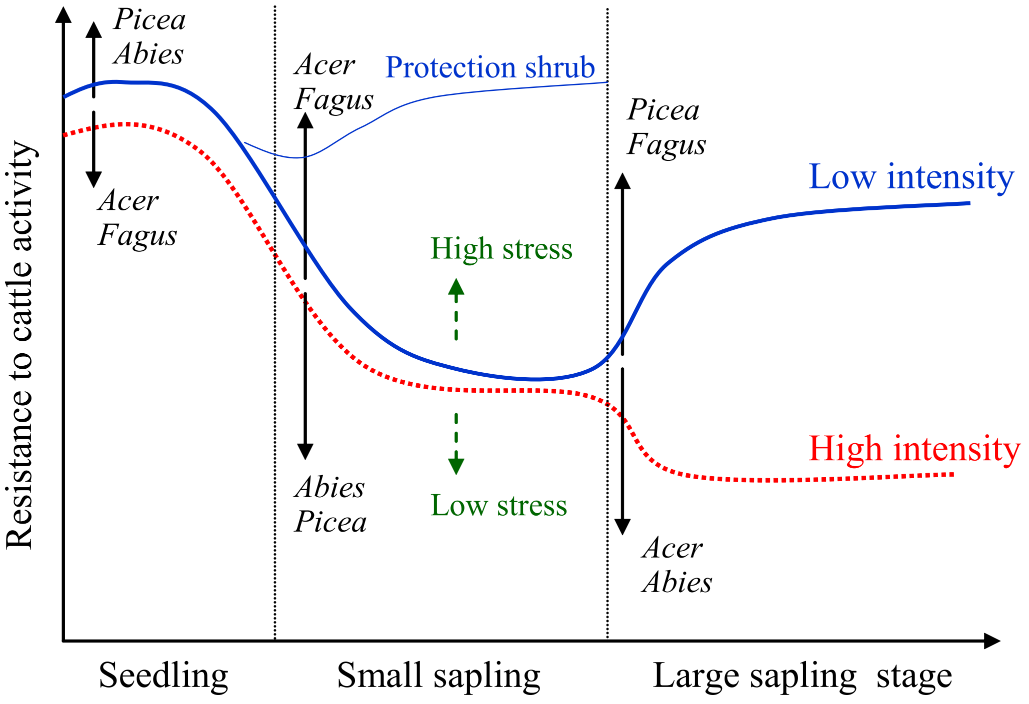

Figure 7.4 Proposed patterns of changes in resistance to cattle activity (escape, defence and tolerance) during the seedling (< 1 year), small and large sapling (1 – 8 years) stage of tree establishment of four species in a mountain wood-pasture. Resistance is based on the differences in survival and growth of seedlings and saplings growing in 'cattle exposed' and 'cattle excluded' areas. Resistance under low (blue, solid line) and high (red, dotted line) grazing intensities is presented (see Table 7.2 for details on grazing intensity values). Solid, black arrows indicate a higher (up) or lower (down) resistance dependent on tree species. Dashed, green arrows indicate a higher or lower resistance dependent on environmental stress. Protection by shrub (thin, blue line) of small saplings will only occur under low grazing intensity (note: the effects of shrub on seedlings and large saplings were not measured in this study).

Although tolerance of browsed seedlings is low due to limited resources, seedlings have a high resistance towards large herbivores. Firstly, other factors such as competition from neighbours, predation by insects and rodents, and overall low resource availability are important factors limiting seedling survival and these factors reduce the relative importance of cattle activity. Secondly, seedlings have higher escape chances than saplings. Especially coniferous species have a lower probability of being browsed due to their small size compared to deciduous species. As seedlings grow and become saplings, browsing escape events will decrease. Moreover, small saplings are less vulnerable to changed environmental conditions related to cattle exclusion than seedlings, enhancing the relative negative effects of cattle activity. Seedlings and small saplings' resistance is expected to have a limited variation among intensities due to an approximately equal off-take rate and mortality chance once found by herbivores and effectively browsed. Deciduous species *Acer* and *Fagus* will have an advantage at the small sapling stage mainly due to lower relative amount of biomass off-take and more flexible growth pattern. As saplings grow, they will become more apparent and rarely escape cattle browsing. The repeated high biomass losses will further decrease resistance. However, at low grazing intensities, resistance of the large saplings will be higher than for the small saplings. If reductions in biomass are not too severe, large saplings will be able to persist better with reduced biomass than small saplings due to higher stored resource availabilities. Especially *Picea* and *Fagus* have a high resistance towards cattle browsing what might be due to higher intrinsic tolerance and/or lower palatability.

The general proposed pattern will change with environmental conditions. Under high stress, such as limited light, nutrient or space availability, tolerance and consequently resistance are expected to increase (Ch. 5). High abiotic (light, nutrients, moisture) or biotic (competition from neighbours, rodents) stress factors limit sapling performance (i.e. survival and growth). Consequently, the biomass needed to compensate after biomass off-take becomes lower. In other words, under low stress conditions, the impact of cattle browsing will be more severe due to high performance of unbrowsed saplings. The degree of tolerance to herbivory is thus not necessarily related to plant performance. As shown in Chapter 5, the saplings that compensated almost for clipping damage often had a lower overall growth than less tolerant saplings with high growth rates in both clipped and unclipped states. Therefore, highly cattle resistant seedlings and saplings might have a lower performance than less resistant plants. Additionally, the nature of surrounding vegetation such as height or palatability will be able to considerably increase resistance through increasing escape chances. Thorny shrubs will protect saplings against browsed, but this process is only effective under low grazing intensities (Ch. 4 and Ch. 6).

7.4 Management implications

Abandonment and intensification of agriculture are expected to continue in the near future (Tilman *et al*. 2002), with drastic consequences for many ecosystems and particularly in wood-pastures, since extensive land use is essential for their conservation. This thesis provides new insights about the likely consequences of changes in cattle grazing intensities and the relative importance of browsing and competition tolerance in the early life stages of trees in wood-pastures. These results should be coupled to policy and management instruments to assist in maintaining these biodiverse ecosystems.

To maintain the tree species diversity in the Swiss mountain wood-pastures, management should be aware that species have different vulnerabilities to cattle activity and this vulnerability varies over the different stages of tree establishment. In years without extreme weather conditions, the deciduous species *Acer* and in particular *Fagus* are less likely to germinate and establish as one-year old seedlings than the coniferous species. However, the coniferous species *Abies* and *Picea* are more sensitive at the small sapling stage. *Picea* and *Fagus* are more resistant at large saplings stage which might explain the higher natural abundance of (browsed) large *Picea* and *Fagus* saplings in wood-pastures (personal observation). The relative establishment advantage of *Picea* during both seedling and large sapling stage may explain why this species is the most common tree species in the mountain wood-pastures of the Swiss Jura Mountains (Gallandat *et al*. 1995).

The difficulty of a sustainable management of wood-pastures lies in the discovery and maintenance of the equilibrium between extensification and intensification as each establishment stage is affected by cattle activity. Planting saplings and nurse plants in order to enhance tree regeneration will only be effective under low grazing intensities. Rodents were responsible for 11 % of the deciduous tree mortality in the planting experiment (*cf.* Chapter 5). Predation by rodents is therefore an important factor affecting sapling establishment in wood-pastures. Moreover, rodent damage by rodents increased when cattle intensity decreased (*cf.* Chapter 3). Consequently, both decreasing cattle intensity and trapping rodents will more effective in enhancing tree establishment. Managers need to consider that livestock exclusion alone in wood-pastures will not maximize sapling performance because it will also increase competitive effects by neighbours and increase abundances of rodent populations. Although grazing intensity management will be important mainly once saplings have emerged above the height of the herbaceous layer, tree seedling emergence and colonisation can be significantly enhanced by postponing the arrival of cattle in spring.

In conclusion, the spatial and temporal heterogeneity (shifting mosaics) of the vegetation structure of the wood-pastures need to be maintained. For this, extensive grazing and maintenance of structures that facilitate tree establishment such as rocks, shrubs and tree stumps are necessary.

7.5 Perspectives

Seed dispersal limitation might have an important role on tree regeneration dynamics (Holl *et al.* 1999; Wang and Smith 2002). Large-seeded species, such as *Fagus*, may be less able to colonise open pasture patches due to lack of animal-seed dispersers and/or heavy seed-predation (Levey *et al*. 2002). The current dominance of *Picea* might be related to its dispersal advantage in distance and quantity due to a large production of small seeds. A study on the seed dispersal dynamics of the common tree species in the wood-pastures should be carried out to provide insight in the spatial and temporal tree regeneration dynamics and tree diversity in wood-pastures.

Contrasting results concerning the role of gaps in pastures on tree seedling establishment were found. Cattle as well as invertebrates and rodents were found to consume seeds and seedlings in gaps and in the intact vegetation. Birds were probably also important seed predators and responsible for decreased seed germination on gaps. More precise insight should be obtained on the habitat-specific impact of different consumers on tree seeds and seedlings via the use of selective exclosures, insecticide and fungicide. Furthermore, a quantification of density, size and distribution of gaps created by cattle under different grazing intensities will help to more precisely define the importance of the role of cattle on seed and seedling stage.

Unexpected results concerning the effect of the abiotic and biotic environment on sapling tolerance (Chapter 5) bring into question the generality of the several hypotheses concerning this topic (see Strauss and Agrawal 1999; Hawkes and Sullivan 2001; Wise and Abrahamson 2005), particularly in relation to the effects of large herbivores. More long-term experiments are required to determine the relative importance of environmental factors (including light, nutrient and soil water availability), and their interactions on sapling tolerance to herbivory.

Aboveground removal of plant parts by large herbivores inevitably affects belowground processes, although these belowground responses have been much less investigated (Holland and Detling 1990; Huntly 1991; Hester *et al*. 2004). It would be interesting to further explore how tree roots are reacting to aboveground biomass releases. Herbivores can indirectly affect decomposer organisms and soil processes through altering the quantity and quality of resources entering the soil (Ayres *et al*. 2004; Harrison and Bardgett 2004). Detailed understanding of multitrophic interactions between populations will help to understand ecosystem processes and maintain endangered systems (Wardle *et al*. 2004).

One of our biggest constraints, as in many ecological field studies, was the short-term character of the field experiments. In particular, the long-term monitoring of survival and growth (at least one year) is needed, as the trees take time to respond to browsing and competition treatments. A long-term experiment, in which seeds, seedlings and saplings are followed for several years under grazed and ungrazed treatments, would certainly help further quantifying the impacts of cattle grazing in wood-pasture systems. However, via several field experiments, I was able to draw conclusions on the relative importance of cattle activity during the different stages of tree establishment. Data were gathered on germination and emergence rates of sown seeds, probabilities of seedlings and saplings of being browsed, and the survival and growth rates of transplanted juvenile trees of different sizes during different months and years. Several manipulations made it possible to understand the relative importance of one or several factors and their interactions. I manipulated a) the grazing intensities via exclosures and different stocking rates, b) the sapling biomass via clipping, c) the competition from neighbours via mowing and herbicide treatments, d) light availability via shade nets, and e) the neighbourhood of the saplings via plantation of shrubs. Through the use of statistical models, empirical evidence was assessed and the effects of cattle on tree regeneration in wood-pastures could be quantified. The provided insight into the interactions between cattle grazing and tree establishment in wood-pastures will contribute to improve ecological theory and models, in addition to informing the management and conservation of wood-pasture systems.

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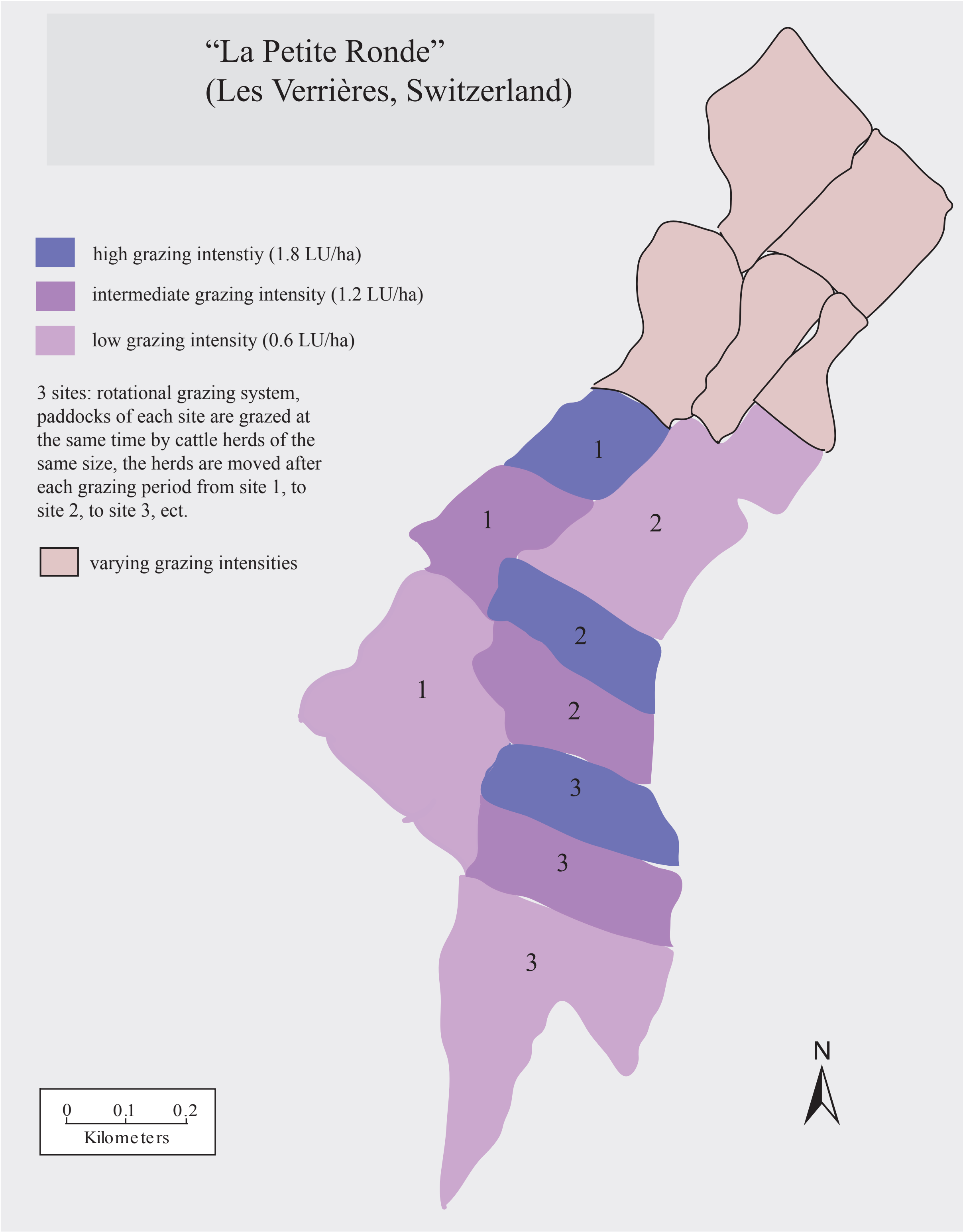
Appendices

APPENDIX 1

Picture 1 Study site ‘La Petite Ronde’.

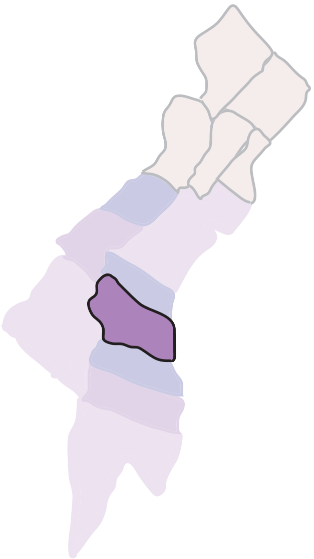
APPENDIX 1

Study site: La Petite Ronde
(Switerland, Les Verrières, 6°27’26” E, 46°56’22”N, 1125 m a.s.l.)



3 sites: rotational grazing system, paddocks of each site are grazed at the same time by cattle herds of the same size, the herds are moved after each grazing period from site 1, to site 2, to site 3, ect.

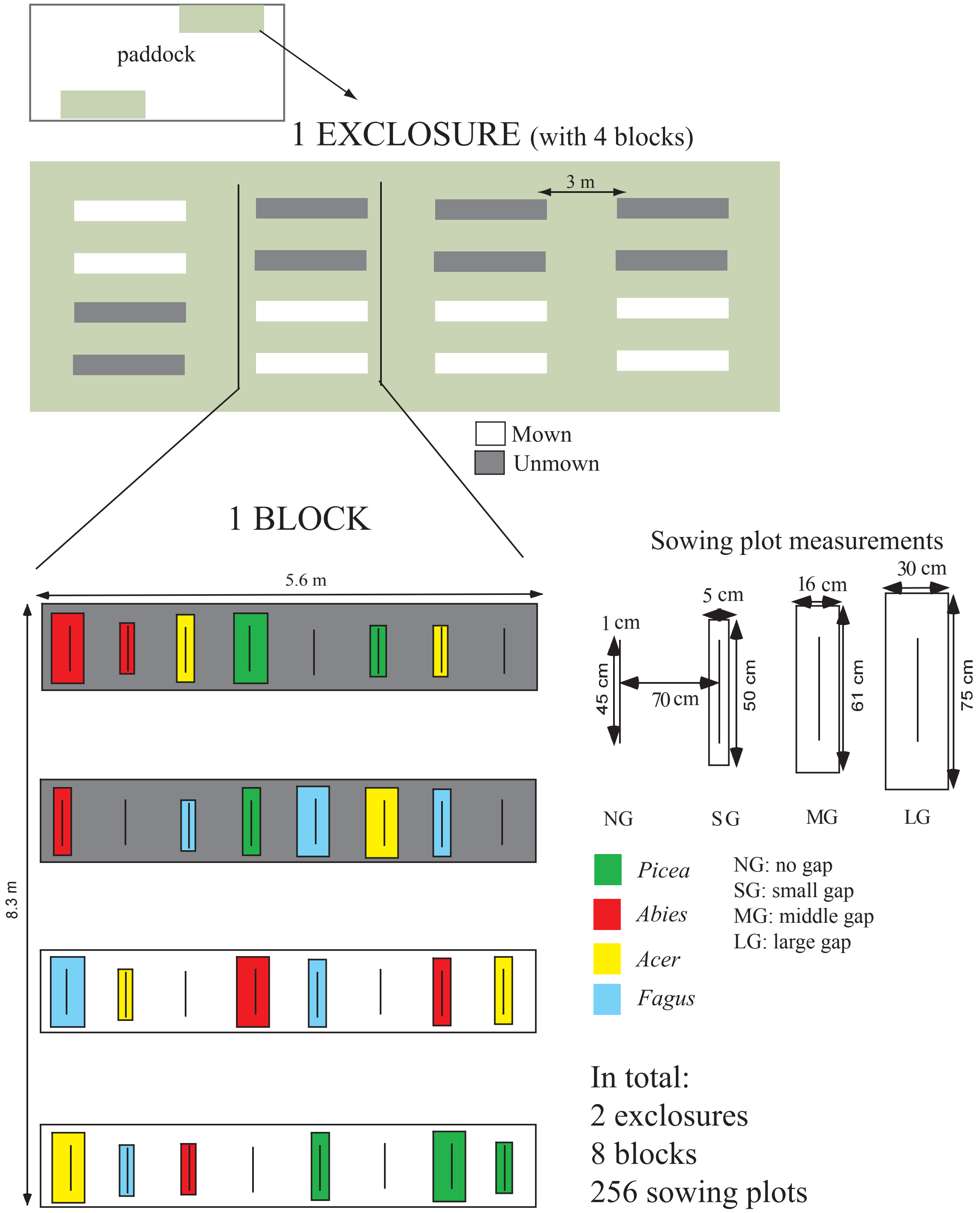
APPENDIX 2



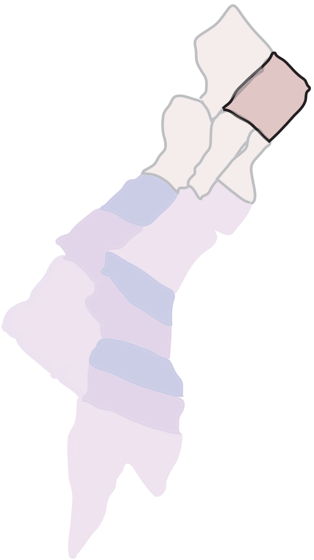
Picture 2 A middle-sized gap (MG) with emerged *Fagus* seedlings (Chapter 2)

APPENDIX 2

Experimental design of Chapter 2: Competitive effects of herbaceous vegetation on tree seedling emergence, growth and survival: does gap size matter?



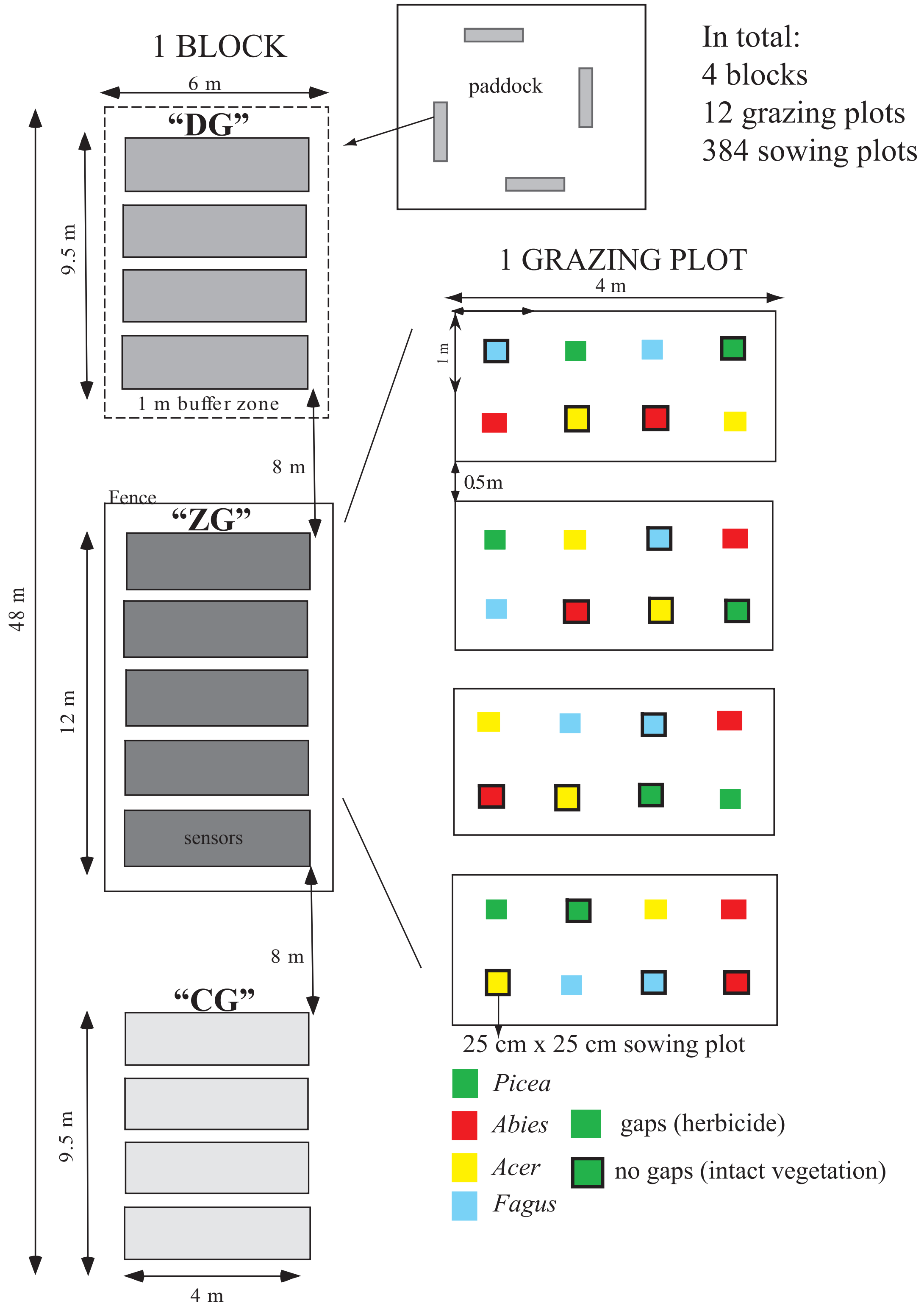
APPENDIX 3



Picture 3 Two gaps (25 cm x 25 cm) with emerged *Fagus* (left) and *Acer* seedlings (right) (Chapter 3).

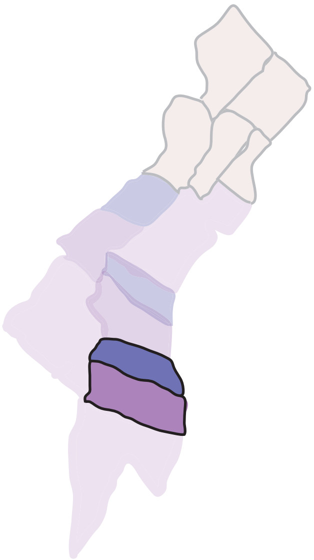
APPENDIX 3

Experimental design of Chapter 3: Effects of herbaceous neighbours and cattle grazing disturbance on first-year seedling establishment



ZG: Zero grazing plot (0 LU days ha^{-1})
DG: Delayed grazing plot (120 LU days ha^{-1})
CG: Continuous grazing plot (198 LU days ha^{-1})

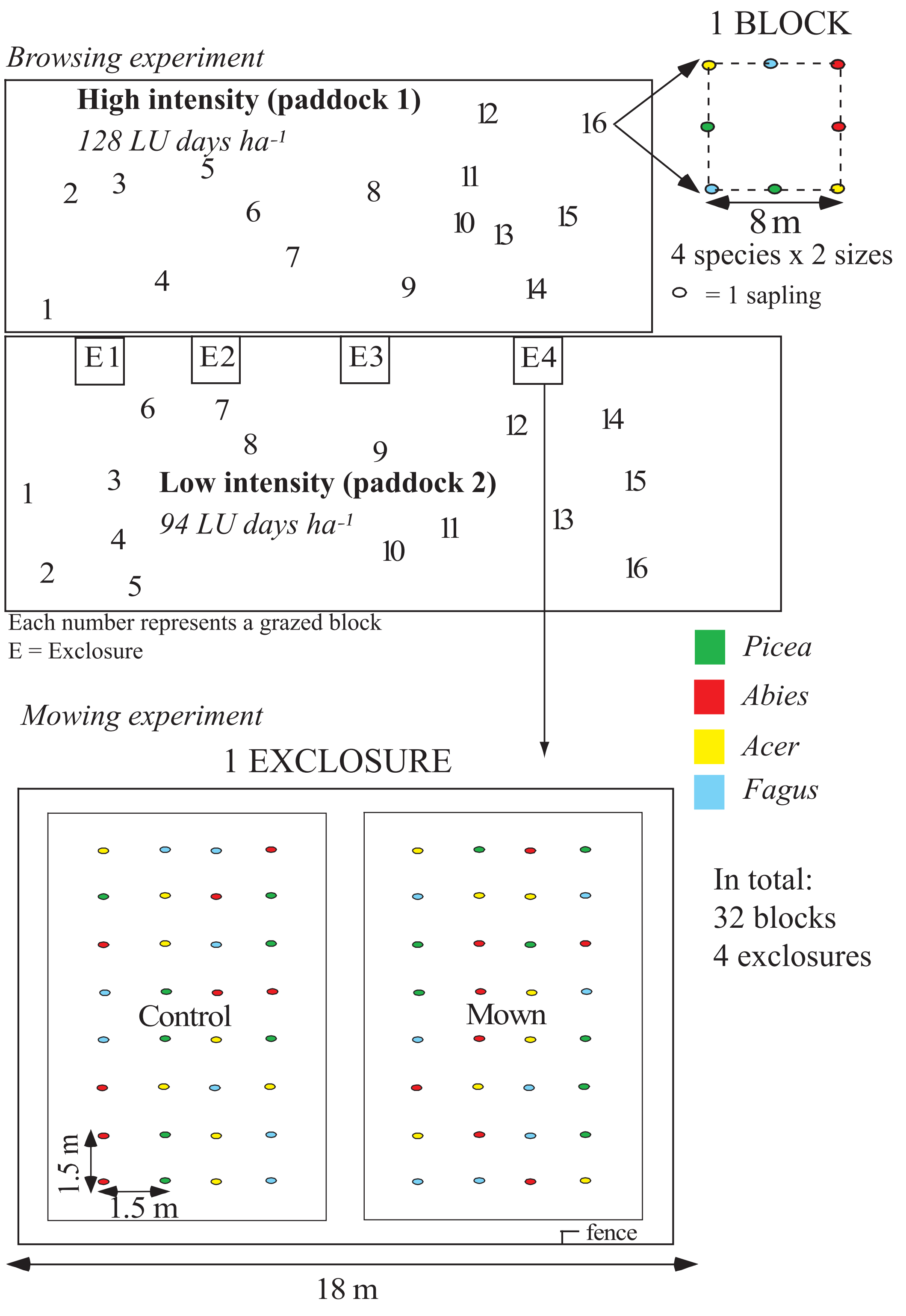
APPENDIX 4



Picture 4 A planted large-sized *Abies* sapling before (left) and after (right) being browsed by cattle (Chapter 4).

APPENDIX 4

Experimental design of Chapter 4: Short-term effects of cattle browsing on tree sapling growth in mountain wooded pastures



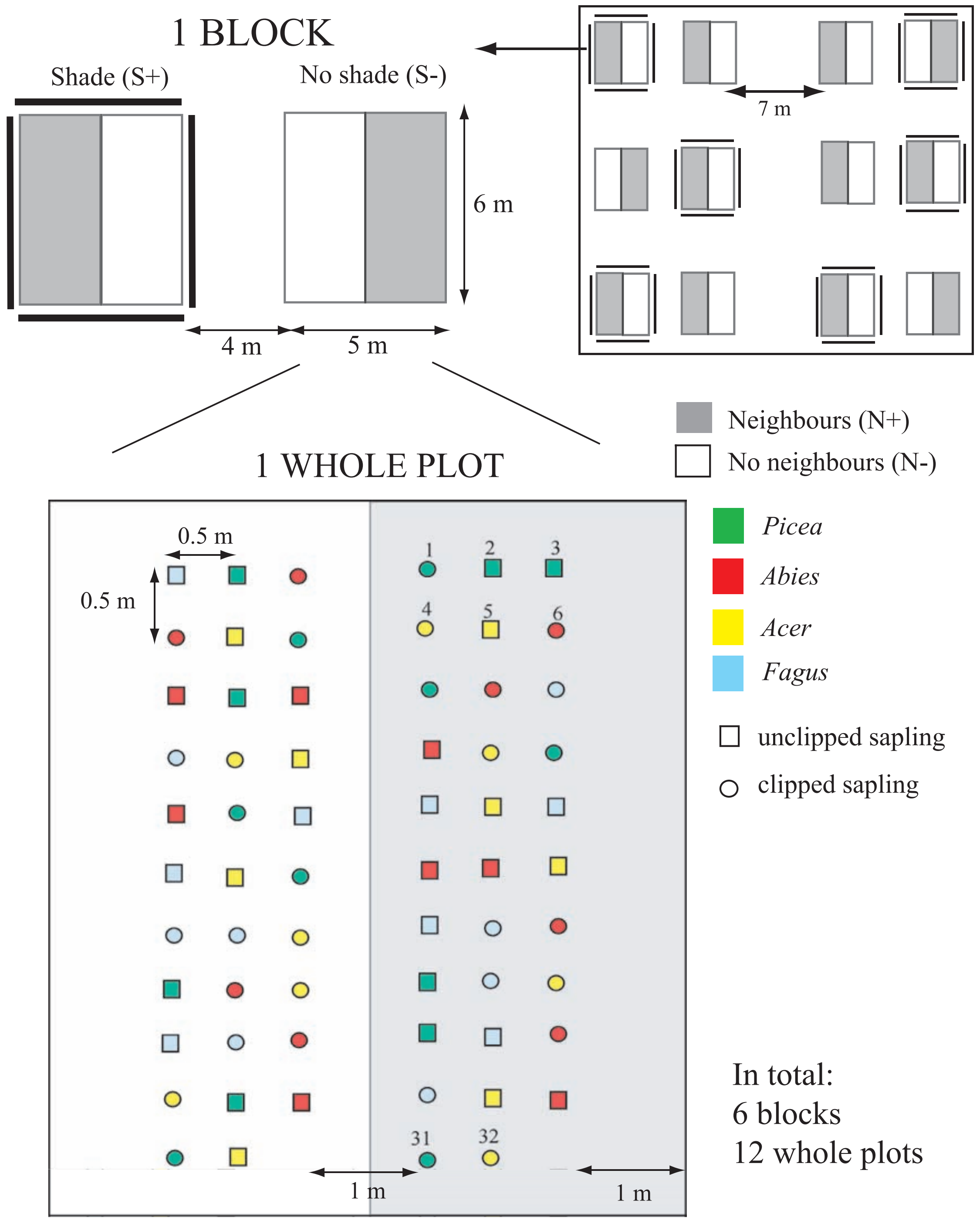
APPENDIX 5

Study site: La Frétaz
(Switzerland, Bullet, 6° 34’ 30” E, 46° 50’ 30” N, 1200 m a.s.l.)

Picture 5 Six blocks laid out in an exclosure at the study site ‘La Frétaz’. Each block exists out of a shade, neighbour removal, simulated browsing and species treatment (Chapter 5).

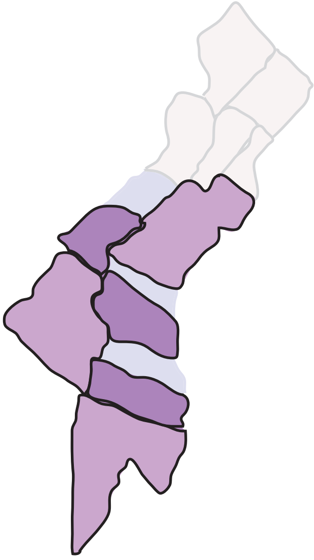
APPENDIX 5

Experimental design of Chapter 5: Interactive effects of simulated summer browsing, shade and herbaceous neighbours on tree sapling tolerance



In total:
6 blocks
12 whole plots

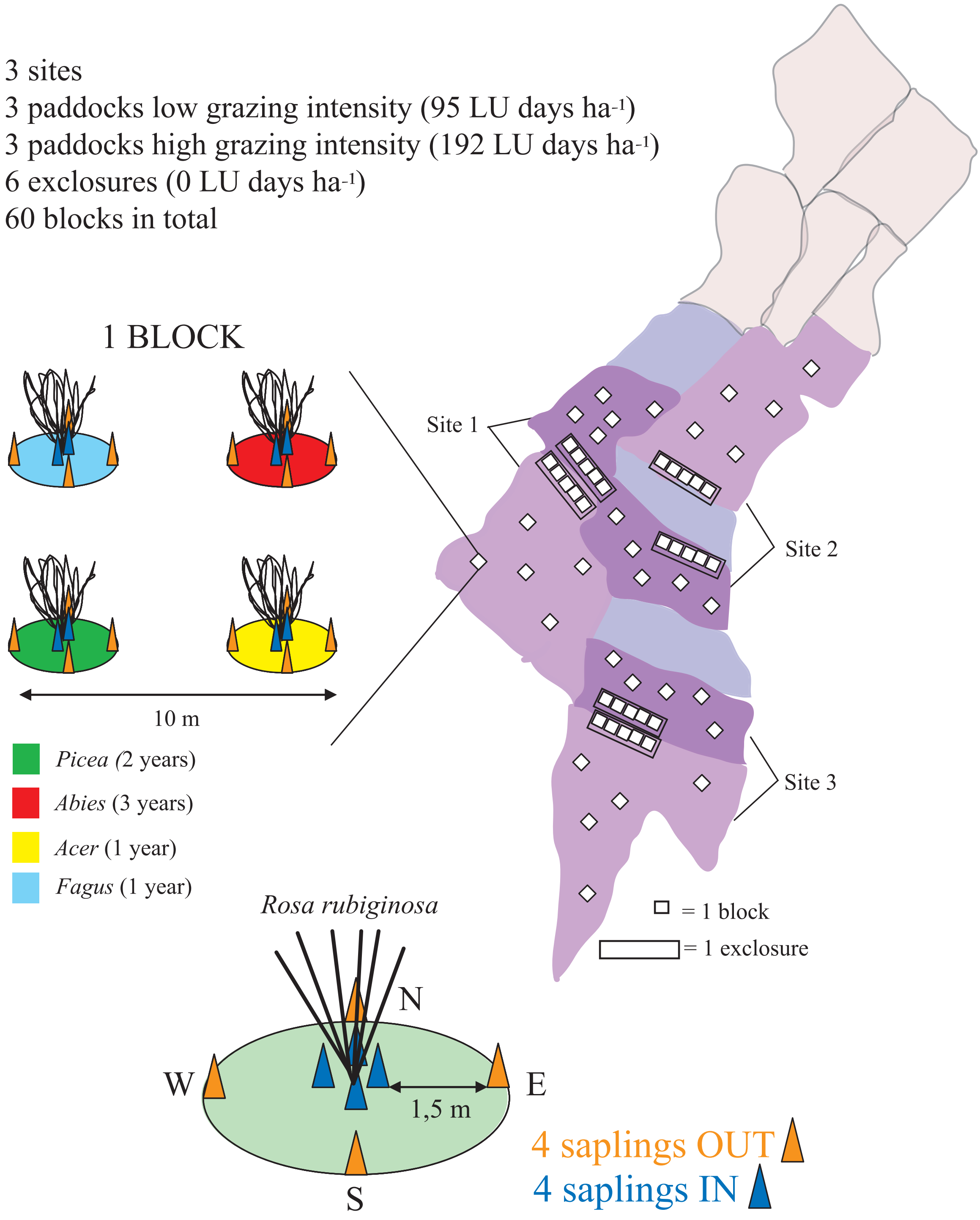
APPENDIX 6



Picture 6 A two-year-old heifer grazing around the thorny *Rosa rubiginosa* shrub (Chapter 6).

APPENDIX 6

Experimental design of Chapter 6: Tree species-specific responses to facilitation by a thorny shrub along a grazing intensity gradient



Curriculum vitae

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Research interests

Grazing ecology, large herbivores, community ecology, plant-animal interactions, biodiversity, facilitation, competition, ecosystem dynamics, foraging behaviour, conservation biology

Education

• 2003 – 2006	Swiss Federal Institute of Technology of Lausanne (Switzerland) PhD research in Ecology
• 2002	Wageningen University (The Netherlands) Post graduate project in Ecology
• 1997 - 2001	Ghent University (Belgium) B.Sc. and M.Sc. Biology-Zoology
• 1991 -1997	Onze-Lieve-Vrouw Ter Engelen high school (Kortrijk, Belgium) Option Latin-Sciences

Research experience

· 2003 - 2006	The influence of cattle activity on tree regeneration in wood-pastures. PhD-research, Laboratory for Ecological Systems ECOS, EPFL and Swiss Federal Research Institute WSL, Lausanne, c/o EPFL (Switzerland) *Supervisors*: Prof. Alexandre Buttler and Dr. François Freléchoux
· 2002	The survival of oak seedlings under grazing: the importance of associational resistance and herbivore size. Post-graduate research project, Wageningen University (The Netherlands), Department of Plant Ecology and Nature Conservation *Supervisors*: Prof. Dr. Han Olff and Drs. Liesbeth Bakker
· 2000 - 2001	The influence of lactation and gestation on the grazing behaviour of donkeys and Shetland pony's in the coastal dunes. Master thesis, Ghent University (Belgium), Department of Terrestrial Ecology *Supervisors*: Prof. Dr. Maurice Hoffmann and Drs. Indra Lamoot

Work history

. Sept-Dec 2006	scientific collaborator (WSL, Lausanne)
· May 2002	teaching assistant of field excursions (Wageningen University)
· August 2001	data-processing at the Institute for Nature Conservation (Brussels)

Computer skills
- Microsoft office, Access, Adobe.
- Program R, S+ and SPSS for statistical analyses

Language skills
- Dutch: mother language
- English: very good knowledge
- French: very good knowledge
- German: basic knowledge

Courses within Graduate School
- Analysis of Variance (Ghent University, Belgium)
- Biodiversity and Species Interactions (University of Neuchâtel)
- ArcGIS – Geodatabase course (ETHZ, Zürich)
- Functioning of Boreal Forest Ecosystems (SLU, Umea, Sweden)
- Scientific communication course (EPFL, Lausanne)
- An introduction to the practice of statistics using R (University of Neuchâtel)
- Applied statistical regression modelling using R (University of Neuchâtel)

Papers in peer reviewed journals

- Bakker, E.S., Olff, H., **Vandenberghe, C**., De Maeyer, K., Smit, R., Gleichman, J.M. & Vera, F.W.M. (2004) Ecological anachronisms in the recruitment of temperate light-demanding tree species in wooded pastures. *Journal of Applied Ecology* 41: 571-582.

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- **Vandenberghe, C**., Freléchoux, F. & Buttler, A. Interactive effects of simulated browsing, shade and herbaceous neighbours on tree sapling performance. *In preparation.*

- Freléchoux, F., **Vandenberghe, C**., Smit, C., Pohl, M. & Buttler, A. Tree species-specific responses to facilitation by a thorny shrub along a grazing intensity gradient. *In preparation*

- **Vandenberghe, C.** Effects of herbaceous neighbours and cattle disturbance on first-year seedling establishment. *In preparation.*

Seminars and presentations/posters at meetings:

- January 2004: Short-term effects of cattle grazing on tree sapling growth in mountain wooded pastures. Internal seminars, University of Neuchâtel, Laboratoire d'écologie végétale, *oral presentation.*

- June 2004: Influence of cattle activity on tree sapling performance in wood pastures. PhD course on the "Functioning of Boreal Forest Ecosystems", Swedish University of Agricultural Sciences (SLU), Umea, Sweden, *oral presentation.*

- November 2004: Influence of cattle activity on tree sapling performance in wood pastures. NCCR PS6 meeting, University of Bern, *oral presentation.*

- February 2005: Short-term effects of cattle grazing on tree sapling growth of Norway Spruce, Silver fir, Sycamore maple and Beech in wooded pastures. Biology 05 meeting, University of Basel, Switzerland, *poster presentation.*

- April 2005: Short-term effects of cattle grazing on tree sapling growth in mountain wooded pastures. NCCR Plant Survival International Conference, Leysin, Switzerland, *poster presentation.*

- September 2005: Effects of grazing intensity and associational resistance on tree sapling growth and survival. British Ecological Society, Annual Meeting, University of Hertfordshire, England, *poster presentation.*

Other publications

- L'influence de l'activité du bétail sur la régéneration des arbres en pâturage. Freléchoux, F., Vandenberghe, C., Buttler, A. Troxler, J., Jeangros, B & Wohlgemuth, T. *La Fôret*, 2005, août, pp. 48-49.

- Baumverjüngung auf weiden. Freléchoux, F., Vandenberghe, C., Buttler, A., Troxler, J., Jeangros, B & Wohlgemuth, T. *Wald und Holz*, 2006, n° 1, pp. 37-39.

- Des vaches et des arbres. Interview by Bolliger L. *Terre & Nature*, 2006, n° 18, p. 15.