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Gunilla Cassing

Deciduous tree occurrence and large herbivore browsing in multiscale perspectives

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Abstract

Aspen (*Populus tremula*), rowan (*Sorbus auquparia*) and sallow (*Salix caprea*) are deciduous tree species of low economic value for forestry and contribute to biodiversity of boreal forests. The species are rare in managed forest landscapes, and severely browsed by moose. Their recruitment needs to increase to meet requirements of sustainable forestry so factors that affect occurrence need to be indentified. **Paper I** is an exploratory study on distribution of these species in relation to natural and cultural factors. In **paper II** I study moose browsing on saplings, in young forests and the influence of the landscape at three spatial scales: stand (8.6 ± 0.8 SE ha), winter home range of moose (10 km^2) and annual home range of moose (25 km^2). Presence of these rare species was depending on a multitude of factors acting at different spatial scales. The most important variables were soil quality, successional stage, ownership at the stand scale and area of deciduous forest at the landscape scale. Moreover, saplings occurred at low densities in young forests **(paper II)** and most interestingly, saplings occurred most in middle-aged forests (20-80 years) and less than expected in younger forests (<20y) (**Paper I**). Browsing intensity on the different species corresponded with moose food preference and annual home range scale was most relevant for understanding browsing. Browsing on rowan was highest where the volume of deciduous food and overall young forest area were low. Browsing on birch increased when pine volume and mean patch size of young forest increased, whereas browsing on aspen was negatively related to the same variables. Thus, my results strengthen the idea that food selection is a scale-dependent process and that trade-offs between food and cover may exist for moose. I conclude that the presence of deciduous species was a result mainly of soil quality, landscape context, forest management intensity and herbivore browsing and that the distribution of food for moose at landscape scales similar to or larger than their home range may be useful for predicting browsing on the stand scale. I propose that deciduous forests may be valuable predictors of regeneration potential in the nearby forested landscape, and that understory deciduous sapling in middle-aged forests may be important to promote restoration and conservation actions.

Contents

List of papers

This thesis is based on the following papers which are referred to by their Roman numerals.

I. Cassing, G. Mikusinski, G. and Widén, P. 2009. Occurrence of deciduous trees in west-central Sweden in relation to ecological and cultural attributes at site and landscape scales. *Manuscript.*

II. Cassing, G. Greenberg, L.A. and Mikusinski, G. 2006. Moose (*Alces alces*) browsing in young forest stands in central Sweden: a multi-scale perspective. Scandinavian Journal of Forest Research 21: 221 – 230.

Introduction

Forest management, biodiversity and deciduous trees

Throughout the boreal region the composition and structure of landscapes and forest stands have been altered by industrial forestry (Franklin and Forman 1987, Angelstam 1997, Kuuluvainen 2002). Forests alterations involve reductions of old growth forest, altered age class distributions and habitat isolation as well as changes in habitat quality e.g. reduction of structural components and altered tree species composition (Essen et al.1997, Kouki et al. 2001). Moreover, forest practices have led to a lowering of the mean age of many forest stands and reduced the size of forest patches, which in turn have affected the availability of habitats for animals (Edenius et al. 2002a). Landscape ecology, the study of ecological processes in relation to the temporal and spatial context of the environment has been of major interest for foresters for only a few decades (Turner 1989). Thus, the effect of landscape structures on organisms is often poorly understood. Typical aspects of the landscape that often is considered include patch size, the proportion of different habitats, the distance between habitats and matrix context.

In Scandinavia, humans have used forests for several hundreds to thousands of years (Wieslander 1936, Kuusela 1990, Östlund 1994). During the mid 1900´s clear-cutting became the dominant harvesting method transforming the heterogeneous landscape mosaic created by natural disturbance regimes into a landscape mosaic largely composed of homogenous, even aged and single species stands (Essen et al. 1997, Kouki et al. 2001, Axelsson et al. 2002). From the 1960´s to the 1980´s, the amount of young forest stands in Sweden was almost doubled due to clear cutting (Strandgaard 1982). Consequently, the proportion of young successional stands with planted conifers and naturally generating pioneer deciduous trees like birches (*Betula spp*), aspen (*Populus tremula*), rowan (*Sorbus auquparia*) and sallow[*] (*Salix caprea*) increased. The intense management for timber and pulpwood has focused forest production on coniferous species, mainly Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Remröd 1991). Deciduous tree species have been perceived as worthless competitors with little economic value and therefore sometimes targeted for active eradication. Research and management have until recently been focused on different measures to reduce competition from deciduous trees and have included active measures as selective felling, girdling, notching, herbicide spraying, and active suppression of forest fires and flooding (Lund-Hoie and Andersen 1993, Zakrisson 1985, Götmark et al. 2005a) All of these,

[*] The common name sallow is used in this thesis for *Salix caprea* except in **Paper II** where I used the common name goat willow for the same species.

as well as intense browsing from large herbivores led to the decline of deciduous trees in boreal Scandinavia (Kuuluvainen 2002, Hellberg 2004). A high proportion of pioneer deciduous species is, in naturally dynamic boreal landscapes, characteristic of early and intermediate successional phases after disturbance. These natural successional stands are among the most species-rich habitats in boreal Fennoscandia (Esseen et al. 1997, Kouki et al. 2001). The prevailing view is that deciduous trees were a more common component of boreal forests prior to industrial forestry even if their distribution and abundance varied both temporally and spatially (Olsson 1992, Angelstam 1997, Björse and Bradshaw 1998, Axelsson et al. 2002, Hellberg 2004). For example, in the primeval forests 20% of stems were deciduous as compared to 5% today (Zakrisson and Östlund 1991).

Deciduous trees are hosts for a very high number of species of conservation value in Sweden (Berg et al. 1994) and many species dependent on deciduous trees face extinction (Gärdenfors 2000, Nitare 2000). Deciduous trees such as aspen, rowan and sallow are known to be important substrates for several epiphytic bryophytes, lichens, fungi and insects in the Scandinavian boreal forest (Ehnström and Waldén 1986, Kuusinen 1996, Martikainen et al. 1998). Several birds are also associated with habitats rich in deciduous trees and dead wood, e.g. woodpeckers and other bird species (Angelstam and Mikusinski 1994, Jansson 1999, Åberg 2000). Restoration of deciduous rich forests in the boreal landscape is regarded as one of the main needs at present to preserve biodiversity in Swedish forests. For example objectives of the Swedish Environmental Protection Agency include interim targets directed at increasing the area of mature forest with a large deciduous element by at least 10% and at increasing the area regenerated with deciduous forest (Anon. 2001).

Management intensity is suggested to be a major factor influencing the conservational status of managed forests; supposedly because the more mechanized forestry management is the fewer conservation actions that are taken (Eckerberg 1986, Olsson 1992). However, numerous natural and cultural factors, such as soil conditions, light-exposure, topography, silvicultural actions, old-field abandonment and large herbivore browsing are suggested to affect regeneration of deciduous trees in Swedish boreal forests today (Rytter 1998, Axelsson et al. 2002, Mikusinski et al. 2003, Götmark et al. 2005a, Rytter and Werner 2007).

Large herbivore browsing

Large herbivores can impose substantial damage to young trees in boreal and temporal forests (Cederlund and Bergström 1996, Bergqvist 1998, Hessl 2002). Browsed saplings may either be suppressed or die, and rarely grow into mature trees (McInnes et al. 1992, Esseen et al. 1997, Angelstam et al. 2000). In Scandinavia, browsing from large herbivores mainly affects forestry production of Scots pine, but also regeneration of many deciduous species such as birch, aspen, rowan and sallow (Cederlund and Bergström 1996, Angelstam et al. 2000). The increase in young forest area during the 1900´s and hence food availability for large herbivores is considered the main factor behind a drastic expansion in these herbivore populations over the same time period (Strandgaard 1982, Cederlund and Bergström 1996). However, several other factors such as new hunting regulations, extirpation of large predators and decreased competition from livestock, earlier influenced large herbivore populations (Cederlund and Markgren 1987, Cederlund and Bergström 1996). Moose (*Alces alces*) and roe deer (*Capreolus capreolus)* are the primary large herbivores in Scandinavian forest landscapes, with moose being the main browser (Cederlund 1983, Bergström and Hjeljord 1987, Andrén and Angelstam 1993, Mysterud 2000). In Scandinavia, moose preferentially feed on rowan, willow (*Salix spp.*) and aspen, although their diet is typically dominated by the more abundant Scots pine and birch (Bergström and Hjeljord 1987, Hjeljord et al. 1990, Cederlund and Bergström 1996). Rowan and aspen are also the woody species most preferred by roe deer, but they feed mainly on herbs and shrubs (Mysterud 2000). Thus, moose is considered the main browser on woody species.

The browsing problems associated with moose mainly occur in young pine stands (5-15 years old) and at trees that are 0.5-2.5 meters in height (Bergström and Hjeljord 1987, Anon. 2002a). Because of reduced wood production and timber quality, and consequently economic loss, large herbivore browsing on conifers has been studied for a long time (Lavsund 1987, Bergström and Hjeljord 1987, Kardell 1999). Recently browsing on deciduous species in a biodiversity context has become a center of attention (e.g. Angelstam et al. 2000, Götmark et al. 2005ab, **Paper II,** Edenius and Ericsson 2007).

Landscape, deciduous trees and browsing.

The spatial context of a landscape refers to the spatial arrangement of habitats over a broad spatial scale and is believed to have a major impact on population and community level processes which is a major area of interest for wildlife and forest managers (Turner 1989, Lidicker 1995, Andrén 1997). Landscape ecology has traditionally been used in understanding why the existence of some species is threatened. For deciduous forests a landscape approach has been used to study threatened species of lichens (Hedenås et al. 2007, Hedenås and Ericsson 2008) and woodpeckers (Mikusinksi 1998, Mikusinski and Angelstam 2004, Angelstam et al. 2002) and for more common bird species such as long tailed tit *(Aegithalos* *caudatus)* (Jansson, 1999) and hazel grouse (*Bonasa bonasia*) Åberg 2000). There is even an interest using a landscape approach when studying large herbivore browsing and deciduous tree recruitment (Mikusinski et al. 2003, Götmark et al. 2005ab, Edenius and Ericsson 2007, Zackrisson et al. 2007).

Both natural and cultural features of the landscape such as reforestation on abandoned fields (Lindbladh 1999, Mikusinski et al. 2003), disturbance regimes and environmental conditions along watercourses (Naiman et al. 1993), vegetation zones, where for example vegetation period and other climatic and nutritional conditions vary, and proportion of different habitats are of interest when studying deciduous trees (Edenius and Ericsson 2007). From the pioneer characters of species such as aspen, rowan and sallow, one would expect a positive relationship with young forests but these are also main browsing habitats for moose and thus related to severe browsing (Lavsund 1987, Anon. 2002a). Accordingly, at present it is believed that deciduous species mainly occur in mixed forest/agricultural landscapes, along the shores of lakes and watercourses and as remnant stands at steep sites where forestry and browsing have been hindered. This contrasts with the situations in the past, where deciduous trees occurred both scattered in the woods but mainly as stands after disturbance (Essen et al. 1997, Hazell 1999, Löfgren and Andersson 2000). Thus, to maintain biodiversity and above all, to assure proper regeneration of deciduous trees in today’s forests we need to better understand the influence of different factors such as both site characteristics and landscape features on the occurrence of deciduous tree species.

It has been stressed that studies on large herbivore browsing would benefit from incorporation a landscape perspective (Senft et al. 1987, Andrén and Angelstam 1993, Hobbs 1996, Bergquist 1998, Angelstam et al. 2000). Animal habitat selection is determined by mechanisms that operate on various spatial and temporal scales, and thus an animal’s decision to use a food patch may depend on both the availability of food within the patch and the spatial arrangement of food patches at broader spatial scales, such as animal’s home range (Johnsson 1980, Powell 2000). Hence, habitat patches of similar quality but embedded in different landscapes may differ greatly in their use by animals (Burges and Sharp 1981, Addicott et al. 1987, Fahrig and Merriam 1994). Numerous studies have suggested that landscape patterns affect feeding site selection by large herbivores and that foraging strategies vary across spatial and temporal scales (Senft et al. 1987, Hobbs 1996, Angelstam et al. 2000, Edenius et al. 2002b). The primary approach used to decrease browsing pressure has been to reduce and regulate ungulate population densities (Schmitz and Sinclair 1997) as done in Sweden for both moose and roe deer from late 1980´s. However, the spatial pattern of browsing damage for pine is unevenly distributed in the forest i.e. the amount of young forests with intense browsing pressure differs between areas with similar moose densities (Hörnberg. 2001ab). Thus, the relationship between moose density and damages caused by browsing is not straightforward and interactions between food availability and landscape pattern are suggested as possible explanations to this pattern (Cederlund and Bergström 1996**,** Hörnberg 2001ab, Bergstöm et al. 1995). Thus, a landscape-based approach that considers both food availability and landscape structure may improve our understanding of habitat use and browsing by moose in managed forests.

Objectives

The two main questions addressed in this thesis were

I: Where do saplings and trees of deciduous species occur in relation to site characteristics and landscape features?
II: Where does intense browsing on deciduous species occur in relation to site characteristics and landscape features?

The ultimate goal of this thesis is to improve our understanding of the requirements and potential for restoration of aspen, rowan and sallow in boreal landscapes. In **Paper I** the occurrence different height-classes of deciduous species is explored in relation to relevant ecological and cultural conditions: nutritional conditions i.e. site quality, successional stage, topography i.e. elevation and slope, vegetation zone, landscape context i.e. distance to agriculture, distance to water, and area of different forest types as well as management i.e. ownership and former cultural land use.
In **Paper II** I examine if structure and composition of the vegetation at different spatial scales influence moose browsing intensity in young forest stands. Because I assumed that moose habitat selection was a scale-dependent process, I examined stand variation in browsing intensity in relation to variables that reflect availability of moose's preferred browse and the spatial context of the landscape at three different spatial scales 1) the stand (8 ha), 2) the winter home range of moose (10 km^2) and 3) the annual home range of moose (25 km^2).

Methods

Study area

Both studies were conducted in the boreal region of Sweden in Värmland County (Fig. 1), that covers 17, 350 km^2 of which 74% is productive forest (annual growth is > $1m^3$ standing volume/ha). Scots pine (36.0%), Norway spruce (49.1%), downy birch (*Betula pubescens*) and silver birch (*Betula pendula*) (10.0%) dominate forests in the region while aspen (1.1%), rowan, sallow and other species (1.9%) constitute only a minor proportion (Anon. 2003). Timber harvest has occurred in this region for hundreds of years, mostly to provide fuel for the mining industry, but also for timber export (Wieslander 1936, Bladh 1995). Large forest companies (37%), private persons (56%), municipalities and church (2%) and others (5%) own forests in Värmland, an ownership pattern generally resembling the pattern for all of Sweden (the corresponding figures are approx. 42% (including state owned forests), 49%, 2% and 7%) (Anon. 2003). No forests are owned by the state in Värmland except for some nature reserves encompassing less than 1% of the forest land. Värmland is also among the regions in Sweden where large herbivore browsing is considered a severe problem, mainly due to damage to young where there is also intense suppression of deciduous species (Hörnberg 2001a, Anon. 1996). Since the 1970´s moose density has been very high, with an estimated maximum of 2.4 individuals km^{-2} in the early 1980´s (Hörnberg 2001a).

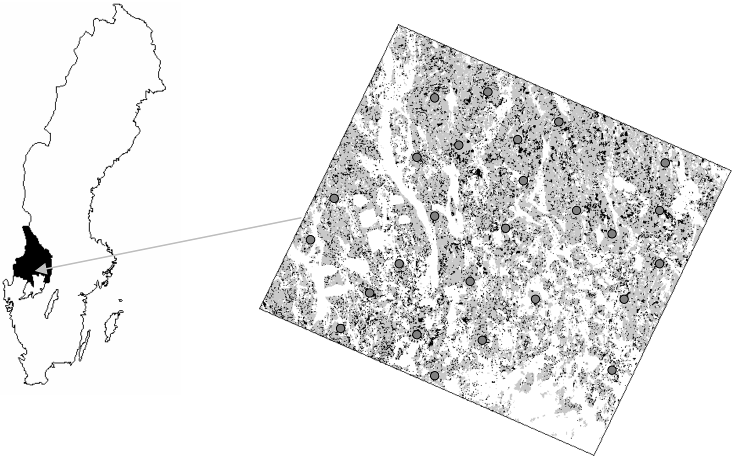

Fig. 1. Left: Location of Värmland, study area in **Paper I,** in Sweden. Right: The arrow denotes the location of study area in **Paper II** and the picture illustrates the heterogeneity of the study area. White=non forested land, grey=forested land and black=young forests. Dots are study stands.

In **paper I** data covered the whole region while the study area (412,000 ha) for **Paper II** was located in the south boreal region, and consisted of 61% productive forest, of which 23% was less than 20 years old. The remaining 39% of the area was bogs, lakes, agricultural land and human settlements. Forest cover was approximately similar throughout the area but slightly less in the south. According to hunting data the moose population was similar both over the area and over time for 10 year period prior to the field examination.

<u>GIS based data</u>

Both studies were mainly based on data from digital data sources that were combined using GIS. All GIS analyses were performed with ArcView 3.2 (ESRI 2000). Data in **Paper I** were derived from a forest survey (in Swedish Skog and Miljö ≈ Forest and Environment) of Värmland conducted by the Regional Forestry Board in 1994, and constituting 16558 systematically distributed (distance≈1 km) circular sample plots located on forest land (r=10 m i.e. 314 m^2) (Anon. 1996). Lakes, mires and open bedrock were not included (often referred to as "non productive" land). Categorical data from the survey used in this thesis included presence-absence of aspen, rowan and sallow for three height classes (1-2 m, 2-4 m, and > 4 m) respectively, stand age, ground vegetation, and former cultural land use. I also included data on ownership, topography and landscape context from e.g. Digital Elevation Models (DEM) for Sweden and GSD-Land and Vegetation Cover database. In particular, I relate the occurrence of aspen, rowan and sallow of two different heights (1-4m and >4m) to 1) successional stage (0-20y, 20-40y, 40-80y >80 y), site quality (low, intermediate, high), elevation (m above sea level) and topographic slope (degrees), 2) the cultural variables reflecting management; former cultural land use (traces of former land use present-absent) and land ownership (Industrial forest owner (IF) or non-industrial owner (NIPF i.e. private persons) 3) the continuous variables reflecting on landscape context at an intermediate scale; distance to nearest agricultural land, distance to water, total forest area, young forest area and deciduous forest area 4) and to vegetation zones (mid-, south- and hemi-boreal zones).

Paper II is based on kNN-database (k Nearest Neighbor) produced by the Swedish University of Agricultural Sciences, combining remote sensing information from SPOT satellite imagery with field data (Reese et al., 2003). The kNN-database used in this study consisted of a series of raster-based layers with information on forest age, tree height and estimated timber volume of tree species with a spatial resolution of 20 m. Volume of young trees and spatial structure were determined at the three spatial scales: stand, winter moose home range and annual moose home range. The stand scale (8.6 ± 0.8 SE ha) represents the specific habitats used by moose and the basic unit for forestry management in Sweden. We selected a 10 km^2 area around each stand as the winter home range scale (WHR) and a 25 km^2 area as annual home ranges (AHR) according to studies of moose home-range in Scandinavia (Cederlund and Okarma 1988, Sweanor and Sandegren 1989, Histøl and Hjeljord 1993, Cederlund and Sand 1994). With both their midpoints at the stand center the two spatial scales were defined as concentric circular areas that did not overlap between study stands i.e. their midpoints were at least 5.6 km apart. Within WHR and AHR circular areas, the area of forests aged 5-15 years, number of patches and mean patch size as well as average tree volume (m^3/km^2) i.e. moose browse in the young forests were calculated.

Field data (**Paper II**)

Vegetation and browsing were measured in 26 young stands approximately evenly distributed in the study area in spring 2002. Young stands were generated from kNN. The study stands were selected by randomly distributed points in the study area. Stands of the following criteria where selected: >50% dominance by pine or deciduous saplings, estimated age of 5-15 years, <5 m in mean tree height, stand size of at least 1 ha and at least 5.6 km from all other selected stands. If the criteria were not met the next stand closest to the coordinate and meeting the above criteria was selected. In approximately 1 circular sample plot per hectare ≤20 random saplings of aspen, rowan, sallow (in **paper II** called goat willow), birch and pine respectively, 0.1-2.5 m tall were examined. Browsing intensity on deciduous saplings was scored as 0=none, 1=slight (<1/3 of the shoots were browsed), 2=moderate (1/3-2/3 of the shoots were browsed) or 3=severe (>2/3 of the shoots were browsed), following the method in the Swedish National Forest Inventory (Hörnberg 2001ab). For pine, the proportion of saplings with browsed or broken apical shoots was used to quantify browsing intensity. Because young stands are used repeatedly by moose i.e. preferred for approx. 10-years, and because both moose density and general landscape patterns are relatively persistent over time, we measured accumulated rather than fresh browsing.

Vegetation composition was examined by counting the number of saplings 0.1-2.5 m tall within each sample plot and averaged across sample plots for each stand. For birch, the number of saplings was often numerous and density was categorized as 1: ≤25 saplings per plot, 2: 25–75 saplings per plot or 3: ≥75 saplings per plot. In analyses, birch density categories 2 and 3 were combined and expressed as the proportion of plots with density categories ≥2.

Results and Discussion

Occurrence of deciduous species in the region

In the entire county rowan saplings were most common and occurred on 16.8% of survey plots, followed by sallow saplings at 11.0 % and aspen saplings at 6.0%. For aspen, occurrence of saplings and trees was similar, with trees at 7.3% of the survey plots, while for both rowan (6.5%) and sallow (4.3%) the trees occurred less than half as often as saplings (**Paper I**).This pattern was consistent when considered for the three vegetation zones separately and accordingly there was a correspondence between occurrence of saplings and trees for each species with the strongest correspondence for aspen. The relatively limited incidence of deciduous species in the region was also observed in the Swedish National Forest Inventory dataset, where aspen and "other deciduous species" (including sallow, rowan, alder and some other rare species) constituted minor parts of the tree volume both regionally and nationally (Anon. 2003). The relative frequency of trees vs. saplings for aspen has been suggested to be a result of severe moose browsing (Anon. 1996). However, the relationship between trees and saplings may also be explained by the species´ different dispersal strategies. Aspen which mainly reproduce clonally showed a stronger relationship between saplings and trees than rowan and sallow and aspen suckers are often restricted to the root system of nearby trees or stumps (parent-trees often < 20 m from suckers (Bärring 1988)) Accordingly, recruitment of rowan rarely occurs near the mother tree presumably as a result of competition from field vegetation, soil pathogens, bird behavior, the need for seed to passage through bird guts and large herbivore browsing (Zywiec and Ledwon 2008).

Occurrence of deciduous species among vegetation zones

Deciduous species also occurred in different proportions among vegetation zones. This north-south increase in the occurrence of deciduous species may be a result of both natural (e.g. nutritional conditions and climate (Essen et al. 1997)) and cultural conditions (e.g. landscape context and land-use history (Bladh 1995, Mikusinski et al. 2003)). For example, summer temperature (climate) may affect the occurrence of aspen through reduced sucker formation and ramet survival (Zakrisson et al. 2007). However, for the observed north-south pattern in **paper I** natural conditions appeared to be insufficient to explain the pattern (Anon. 1996). One could speculate that the pattern may be related to spatial context which has been shown to influence the abundance of deciduous trees (Mikusinski et al. 2003). Although, both southern and northern parts of the region have been used for a long time (Bladh 1995) the northern part of Värmland is largely a forested landscape with only scattered agriculture whereas the southern part is as a mixed landscape. Distance to agricultural land also influenced the abundance of aspen clones in Edenius and Ericsson (2007). I found, strong association between deciduous saplings and trees and sites with traces of former cultural land-use but little effect of distance to agricultural land in **paper I**. Sites with traces of former cultural land-use include old farmland sites that often are more nutrient-rich sites as compared to the surrounding forests, sites with traces of other cultural activities (e.g. slash and burn cultivation and potash production) which correspond to increased light exposure and germination possibilities. Thus I believe: both temporal and spatial variation in land-use may explain this north-south increase in deciduous trees and a main factor behind the difference among vegetation zones is reforestation and colonization of abandoned agricultural land, a process that has been more common in the south (Mattsson (ed) 2005). In addition, deciduous habitats in agricultural areas, not traditionally considered as forest area, may act as dispersal sources, increasing the occurrence of deciduous trees in nearby forests (Särlöf-Herlin and Fry 2000, Mikusinski et al. 2003).

Occurrence of deciduous species and successional stages

A main finding in **Paper I** was that both trees and saplings occurred most in middle-aged forests (20-80 years) and less than, or similar to, expected frequencies in young forests (<20y). This pattern was consistent when tested for saplings and trees in the MLR. Based on the pioneer nature of these species I expected saplings to occur most frequently at young successional stages, which offer both high nutritional availability and extensive light exposure (Hörnberg 2001b, Götmark et al. 2005b). Similarly, in **Paper II** the species were relatively rare in young sites: more than 10 saplings were found at 8 stands for aspen, 11 stands for rowan and 14 stands for goat willow. The implied regeneration in middle-aged successional stages could result from prolonged conditions of the earlier successional stage, favouring recruitment of deciduous species the present successional stage and by a high number of saplings that are suppressed by browsing in the earlier successional stage. Apart from browsing and silvicultural measures also dispersal regimes and shade-tolerance can affect recruitment under canopy.

All three species appear to be more tolerant to shady conditions than previously believed. Rowan recruitment under canopy has been reported several times (Lund-Hoie and Andersen 1993, Linder et al. 1997, Raspé et al. 2000, Holeksa 2000, Zywiec and Ledwon 2008) as well as shade-tolerance in sallow (Rytter 1998, Raspé et al. 2001). Even aspen may be more shade-tolerant than previously thought as Bärring (1988) found aspens 115-130 years of age in a 250 years old spruce dominant forest indicating aspen recruitment under canopy. Moreover, for a related species in Minnesota and Wisconsin, number of shoots emerging from roots increased as stand age developed from 30 to 70, which was interpreted as shade tolerance (Børset 1956). The main reason for aspen being able to recruit under canopy may be its dependence on "mother trees" for clonal regeneration which are more abundant in canopy forests than in young forests. The behavior of perching birds, the main dispersers of rowan seeds, and the use of high forests as post-feeding micro-habitats corresponds with rowan recruitment under canopy (for references see Holeksa 2000 and Zywiec and Ledwon 2008).

Lack of young individuals has been suggested to be a result of insufficient regeneration and the absence of disturbances (Latva-Karjanmaa et al. 2007). Forest fires have been suppressed for several decades and have been implicated as one of the main reason for insufficient regeneration (Zakrisson 1977). Other reasons for insufficient regeneration may be large herbivore browsing and forest management, but even genetics may play a role (Stevens et al. 1999, Zakrisson et al. 2007). Zakrisson et al. (2007) have suggested that genetics may explain why young trees of aspen rarely grow above 1.5 m even after being released from browsing and (Zakrisson et al. 2007). For a related species, the trembling aspen (*Populus tremuloides*), the genetics of a population was drastically affected after a long period without forest fires (Stevens et al. 1999). Thus, the lack of deciduous saplings in forested areas in Scandinavia may be a result of changes in population genetics due to suppressed fire regimes affecting recruitment.

Another factor, large herbivore browsing has been regarded as a main limiting factor for regeneration of deciduous trees (e.g. Angelstam et al. 2000). Locally, herbivore browsing may be so severe that growth and recruitment of deciduous trees is extremely limited (Edenius and Ericsson 2007, Zyviec and Ledwon 2008). Large herbivores mainly use young forests for browsing because mature forests hold less food (Hörnberg 2001b, Edenius and Ericsson 2007). Thus, it has been suggested that high forests may function as refuges from browsing (Ericsson et al. 2001). If this is the case moose can be considered a redistributing agent (Edenius et al. 2002a) affecting successional stages and the composition of tree species. Kalén (2004) suggested that also low browsing intensity can change species composition in habitats.

Paper II demonstrated that browsing intensity on deciduous saplings was very high in young forests in the region, with up to 65% of the stems being highly affected. Moreover, ordering the deciduous tree species from the highest to the lowest incidence of browsing intensity corresponded to the food preferences of moose (Bergström and Hjeljord 1987, Cederlund and Bergström 1996, Hjeljord et al. 1990). Specifically, rowan and aspen, which are preferred items in the diet of moose, were browsed the most intensely and were followed by pine, goat willow and lastly birch.

The pattern of sapling occurrence among successional stages may also be related to silvicultural practices such as cleaning and thinning performed at young forest sites. Accordingly, I found that deciduous trees occurred twice as frequently at NIPF sites than at IF sites and the effect of ownership was consistent over vegetation zones and species when tested in MLR analyses (**Paper I)**. Private landowners are known to leave more stems of deciduous trees than other landowners (e.g. forest companies) after silvicultural cleaning activities (Anon. 1998a). They also use less soil scarification and planting, and more natural regeneration after final harvests than forest companies (Anon. 1998b, Anon. 2003). For example, natural regeneration occurred at 23% of young forests (<1.3m d.b.h.) owned by IF, and at 36% owned by NIPF. Furthermore, voluntary set-asides by private landowners in the southern part of Sweden have a larger deciduous forest component than would be expected by chance (Ask 2002). Nevertheless, the relative effect of browsing and forest management as redistributing agents among successional stages remains to be studied.

Occurrence of deciduous species and landscape features

Both saplings and trees were associated with area of deciduous forest, both over the region and among vegetation zones (**Paper I**). Deciduous forests often grow on sites of high productivity and thus the relationship between occurrence of deciduous species and area of deciduous forest can be confounded with the species´ preference for high soil quality. Accordingly, Strong associations of both saplings and trees were found also with fertile sites (**Paper I**). A similar association between abundance of rowan saplings and fertile sites was recently reported by Hamberg et al. 2008 in Finland. Soil quality has also been suggested to explain regional difference in abundance of aspen clones in northern Sweden (Hedenås and Ericsson 2008). Moreover, soil quality has been proposed as a driving force behind the positive relationship between total ramet density and sapling recruitment in aspen clones because high-quality soil conditions allow more resources to be allocated to above-ground biomass e.g. sprouting and/or growth (Zakrisson et al. 2007). It is with noting that the association between occurrence of deciduous saplings and trees and area of deciduous forest in **paper I** were consistent among vegetation zones with soil quality included in the models, indicating an other effects of nearby deciduous forests such as a source for dispersal (Sarlöv-Herlin and Fry 2000, Mikusinski et al. 2003).

Ericsson and colleagues (2001) found that utilization of aspen by moose was related to landscape composition, with a more intense browsing in aspen stands located in young forests than in old forests. Thus, if browsing was the main factor I would have expected stronger negative associations with area young forest than area of total forest area due to the attractiveness of young forests to large herbivores, but this was not the case in **paper I**. When tested separately deciduous species occurrence were negatively associated with both the area of total forest and area of young forest but the effect was stronger for area of total forest than area of young forest and for trees than for saplings. Edenius and Ericsson (2007) reports that aspen always is browsed severely, and browsing intensity is stronger in forest dominated landscapes compared to mixed landscapes. The negative relationship between occurrence of deciduous species and area of total forest in **Paper I** may result from a lower site quality in conifer-dominated forest as well as browsing and forest management. Accordingly, Götmark et al. (2005b) found that surrounding forest types were important for aspen regeneration, with a negative effect from pine-dominated forests that mainly grow on low productive soils, where deciduous trees are scares. Moreover, area of total forest may reflect several aspects of moose habitat use, such as availability of food and shelter and thus have a stronger influence on occurrence of deciduous species than young forest only (**paper II,** Andrén and Angelstam 1993, Götmark et al. 2005a).

In other analyses, such as the MLR for the whole region, area of young forest was negatively associated with saplings of all species but not for trees, indicating an effect of browsing on saplings throughout the region. When explored over the different vegetations zones, area of young forest was only included in models for saplings of sallow among all vegetation zones and for aspen saplings in the south-boreal zone (**Paper I)**. Thus, the effect on deciduous sapling occurrence from moose browsing differs among vegetation zones and among tree species and influence of moose on occurrence of deciduous species appears to be stronger where availability of deciduous food is low. Moreover, to study effects of moose response to landscape a larger spatial scale than used for area of young forest in **Paper I** may be more suitable (**Paper II**).

Large herbivore browsing and multi-scale perspectives (**Paper II**)

Browsing on aspen in young stands was negatively associated with mean patch size of young forests and volume of pine-browse for both the annual and winter home-range scales. Browsing on birch was positively associated with the same variables at the annual home-range. For browsing on rowan a negative relationship between volume of deciduous browse and total young forest area was found at the annual home-range scale while for sallow no relationship was found. Because young forest area and volume of deciduous species were correlated (**Paper II)** both variables most likely mainly reflect availability of browse (Bergström et al. 1995). The association between browsing on rowan with deciduous food availability in **Paper II** resembles the results of Hörnberg (2001b), where browsing on birch and birch forage availability was negatively correlated. Similarly, Bergström et al. (1995) found that preferred deciduous species, such as rowan, were less browsed when they were common.

The positive relationship between browsing on birch and landscape variables is presumably mainly a result of availability of pine browse because volume of pine is positively correlated to mean young forest patch size. Such a relationship is consistent with the results of Hörnberg. (2001b), where increased browsing on birch corresponded with an increase in pine forage availability. Moreover, the abundance of deciduous species other than birch is generally low in pine-dominated forests, which may mean that birch is susceptible to browsing when the more preferred deciduous browse is scare (Danell and Ericsson 1986, Andrén and Angelstam 1993, Bergström et al. 1995). Thus, these results correspond with the idea that the high food volume in young pine-dominated landscapes influences moose's selection of habitat and food at finer scales (Johnsson 1980, Nikula et al. 2004) and that habitat selection is a scale-dependent process. Similarly, Kalén (2004) demonstrated that knowledge of preference of food species, food availability and landscape effects improve the prediction of spatial consumption pattern.

Interestingly, browsing on aspen was related to the same variables as birch but the relationship was reversed i.e. browsing on aspen decreased as pine volume and mean patch size increased. Hörnberg (2001b) also found an inverse relationship between available pine forage and browsing on a set of species that included aspen. This presumably reflects the fact that aspen rarely grows in the low productive soils where pine dominate (Essen et al. 1997) and their limited occurrence make them difficult to find protecting them from browsing. Moreover, small mean patch size in a landscape often corresponds with relatively large amounts of highly productive edge habitats that are preferred by moose (Burgess and Sharpe 1981, Hunter 1990, Edenius et al. 2002b). Thus, a landscape with smaller forest stands may attract large herbivores even if pine browse availability is lower than elsewhere. Moreover, small forest stands and edge habitats are typical for mixed landscapes, where the amount of deciduous species is usually much higher than in highly forested landscapes (Särlöf-Herlin and Fry 2009, Mikusinski et al. 2003). Accordingly, the cost of travel would be low where young forest patch size is small, which could make moose more disposed to move to the next feeding patch resulting in a higher browsing intensity when compared to areas where young forest patches are large.

Mean size of young forest stands is positively correlated with distance between food and cover (Edenius et al. 2002a) and thus the result for aspen in **Paper II** may reflect moose's need for both food and shelter. Distance to shelter has previously been reported to possibly affect browsing (Hamilton et al. 1980, Andrén and Angelstam 1993). Similarly, in Southern Sweden the amount of cover for ungulates was positively correlated with browsing intensity on oak in a study by Götmark et al. (2005b). Thus, in landscapes with small mean patch size (e.g. mixed landscapes), the proximity between food and cover may result in a higher moose browsing intensity than in landscapes with larger mean patch size (e.g. highly forested landscapes) as a result of trade-offs between food and shelter for ungulates (Senft et al. 1987, Mysterud et al. 1999).

Edenius and Ericsson (2007) argue that aspen always is severely browsed and that browsing intensity is stronger in forested areas compared to mixed landscapes where deciduous forests are more common. This is contrary to the results for aspen in **Paper II** and this discrepancy may have several explanations. First preferred and rare species, such as aspen are not only browsed intensely in relation to their generally low abundance (Andrén and Angelstam 1993, Bergström et al. 1995, Angelstam et al. 2000) but severely suppressed from a long period of large herbivore populations and intense browsing so that almost no recruitment exists in Värmland (Anon. 1996, Hörnberg 2001a, Mattsson (ed) 2005). Thus, both young trees and browsing on them may only exist in mixed landscapes. This is supported by the results in **Paper I** that indicate that deciduous sapling and trees are rare in forested areas. Secondly, rowan and aspen are the woody species most preferred by roe deer, and thus roe deer browsing in some areas may exacerbate the already difficult situation for these suppressed deciduous trees. This may be particularly true in mixed landscapes with low forest cover (Cederlund 1983, Mysterud 2000, Ericsson et al. 2001, Mikusinski and Angelstam 2004). Accordingly, diet quality i.e. diversity of food species for moose was negatively related to roe deer presence (Broman 2003).

Conclusions and management implications

The major findings in this thesis include: 1) A very low abundance of deciduous saplings in young forests (**Paper I and II**) and an unexpected frequency distribution among successional stages with most saplings of aspen, rowan and sallow in middle-aged forests (**Paper I**).

Underestimated recruitment potential in shaded conditions under canopy, dependence on trees for dispersal, severe large herbivore browsing (**Paper II**) and silvicultural actions at young forest sites are possible explanatory factors. 2) Landscapes features may influence both the occurrence of deciduous saplings and trees (**Paper I**) as well as browsing intensity (**Paper II**) 3) Amount of deciduous forest was a main feature of the landscape that deciduous species were associated to. Thus, deciduous forests in the boreal landscape may be good indicators of potential restoration capacity and are likely also important dispersal sources for the deciduous tree species (Sarlöv Herlin and Fry 2000). 4) The distribution of food at landscape scales similar to or larger than the home range of moose may be useful for predicting browsing on the stand scale. The relationship between browsing intensity and landscape differed among food species. Results strengthen the idea that food selection is a scale-dependent process and that trade offs between food and cover may exist for moose.

As pointed out by the results in this thesis, the national trend indicates that aspen regeneration is impaired (Anon. 2002ab). Browsing intensity on a group of species such as aspen, rowan and sallow has increased during the 1990´s even though the size of the moose population has been similar since the early 1980´s (Anon. 2002a). Similarly, the availability of birch and other food species for moose, such as aspen, has declined since the 1980´s (Anon. 2002a). This thesis highlights the need of more studies on sapling occurrence and tree formation of species such as aspen, rowan and sallow in relation to successional stages, landscape context, large herbivore browsing and silviculture and I conclude that one should consider more than moose's need for food when evaluating the mechanisms behind patterns of browsing and effect on deciduous recruitment.

The rarity of aspen, sallow and rowan in boreal landscapes is as described in this study a challenge to forest biodiversity managers. Deciduous trees are valuable substrates for other species and this dependency is linked to tree quality, density of trees and their distribution at the landscape scale. For example, Hedenås and Ericsson (2008) showed for threatened lichens occurring on aspens that species composition differed between agricultural trees and forest interior trees. Thus, conservation and restoration of the deciduous component are crucial in the forested landscape. However, deciduous stands in the agricultural landscape, of low quality for lichens, are important feeding substrate for woodpeckers (Angelstam et al. 2002) and accordingly biodiversity would benefit most if the entire landscape is included in conservation and restoration of deciduous trees (Mikusinski et al. 2003).

Forest owners differ in their management goals and methods and this may have repercussions for recruitment of deciduous trees. For example, reforestation and cleaning actions that inhibit recruitment of deciduous trees are more common for forest companies than for private persons while amount and endurance of conservation measures that sustain deciduous trees in the forests, such as retention of trees at final fellings and voluntary set asides are higher for forest companies than for private persons (Anon. 1998ab, Anon. 2002b). However the commitment to sustainable forestry is strong among forest owners (Hansen et al 1998, Anon.2002b) and during the last 20 years the number of deciduous stems in young forests has increased as well as the area covered by young forest with more than 25% of the stems being deciduous (Anon. 2002a).

In conclusion, the successful restoration of these important structures requires integration of management at different spatial scales (stand-landscape-region) where different stakeholders cooperate in order to assure the continuous recruitment of these trees over large areas (Mikusinski et al. 2007, Edenius and Ericsson 2007). I particular it is important to identify and preserve aspen clones with high sapling density because sapling density is suggested to indicate self-regeneration (Zakrisson et al. 2007). It seems that understory deciduous sapling recruitment in middle-aged forest sites may be important in restoration and conservation actions. Thus, when silvicultural actions are performed in middle-aged managed stands both deciduous trees and understory saplings should be maintained.

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Deciduous tree occurrence and large herbivore browsing in multiscale perspectives

Aspen (*Populus tremula*), rowan (*Sorbus auquparia*) and sallow (*Salix caprea*) are deciduous tree species of low economic value for forestry and contribute to biodiversity of boreal forests. The species are rare in managed forest landscapes, and severely browsed by moose. Their recruitment needs to increase to meet requirements of sustainable forestry so factors that affect occurrence need to be indentified. **Paper I** is an exploratory study on distribution of these species in relation to natural and cultural factors. In **paper II** I study moose browsing on saplings, in young forests and the influence of the landscape at three spatial scales: stand (8.6 ± 0.8 SE ha), winter home range of moose (10 km^2) and annual home range of moose (25 km^2). Presence of these rare species was depending on a multitude of factors acting at different spatial scales. The most important variables were soil quality, successional stage, ownership at the stand scale and area of deciduous forest at the landscape scale. Moreover, saplings occurred at low densities in young forests (**paper II**) and most interestingly, saplings occurred most in middle-aged forests (20-80 years) and less than expected in younger forests (<20y) (**Paper I**). Browsing intensity on the different species corresponded with moose food preference and annual home range scale was most relevant for understanding browsing. Browsing on rowan was highest where the volume of deciduous food and overall young forest area were low. Browsing on birch increased when pine volume and mean patch size of young forest increased, whereas browsing on aspen was negatively related to the same variables. Thus, my results strengthen the idea that food selection is a scale-dependent process and that trade-offs between food and cover may exist for moose. I conclude that the presence of deciduous species was a result mainly of soil quality, landscape context, forest management intensity and herbivore browsing and that the distribution of food for moose at landscape scales similar to or larger than their home range may be useful for predicting browsing on the stand scale. I propose that deciduous forests may be valuable predictors of regeneration potential in the nearby forested landscape, and that understory deciduous sapling in middle-aged forests may be important to promote restoration and conservation actions.

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