Regeneration and early management of birch and Norway spruce mixtures in Southern Sweden

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Abstract

Regeneration involving birch and Norway spruce is the most common mixture on clearcuts in southern Sweden. Sometimes the mixture is unintentional, and the naturally regenerated birch is often regarded as a weed-species in planted Norway spruce monocultures. In other cases, the additional seedlings from spontaneous natural regeneration are, perhaps, not planned for, but are still used, as a convenient way to create mixed forests with management for production and other services. The objectives of the research described in this thesis all refer to the establishment and early management of mixtures with planted Norway spruce and naturally regenerated birch. Hypotheses were tested in field experiments in the counties of Kronoberg and Halland. A better knowledge of seed supply, by estimating seed sources and seed dispersal, could be used when planning future stands and in the choice of management. The effect of soil scarification on seed emergence and seedling survival was tested in field experiments and modeled together with distance to seed supply. The combination of spatial information about standing volume and specific site variables produced birch regeneration estimates that could be useful for practical management and planning. Once the seedling population was established, after three to five years, the density, height structure and species composition were tested as variables for further selections in precommercial thinnings. The retained stems, 1000-3000 trees ha^{-1}, responded positively to a reduction in competition even when stand heights were as low as 1-2 meters. The size of neighbors was more important than the species for the individual growth of both birch and Norway spruce. The competition release in the early stand is important if the target is to retain a mixed forest throughout the full stand rotation, otherwise the retained birches will have difficulty competing with the planted Norway spruce in later stages of the rotation. Other common broadleaved species and pine regenerate on the same clearcuts but the current browsing pressure from ungulates reduces the possibility to allow these species to be present in the future stand.

Keywords: seed dispersal, natural regeneration, soil scarification, precommercial thinning, mixed forest

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Vi gick stigen. En massa barr hade fallit under natten eller tidigare, det var oerhörda mängder. De flesta talar lyriskt om naturen, utan att tänka på all denna materia som den består av och som ofta utgöra rena hinder. Man kan plötsligt få syn på det, då förstår man inte var man har varit tidigare. I någon fotobok med blommor kanske, men det mesta är sannerligen inte blommor.

Thomas Tidholm. Semester med Sven

Diversity is the rule and monotony the exception.

John L. Harper. Population biology of plants, p 237.

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Holmström, E., Karlsson, M. & Nilsson, U. Modeling birch seed supply and seedling establishment during forest regeneration. (manuscript)

II Holmström, E., Ekö, P.M., Hjelm, K., Karlsson, M. & Nilsson, U. Natural regeneration on planted clearcuts – the easy way to mixed forest? (manuscript)

III Holmström, E., Hjelm, K., Karlsson, M. & Nilsson, U. Multiple scenario analysis of precommercial thinnings in mixed stands. (manuscript)

IV Holmström, E., Hjelm, K., Johansson, U., Karlsson, M., Valkonen, S., & Nilsson, U. (2015). Pre-commercial thinning, birch admixture and sprout management in planted Norway spruce stands in South Sweden. Scandinavian Journal of Forest Research, DOI:10.1080/02827581.2015.1055792

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The contribution of Emma Holmström (EH) to the papers included in this thesis was as follows:

I EH is the main author. Matts Karlsson developed the first versions of the model. EH and MK undertook separate parts of the data analysis and model construction. EH wrote most of the manuscript with assistance from the co-authors.

II EH is the main author. Field experiments were planned and performed by the supervisors for several years before EH began work on this research. EH carried out field measurements and data analysis. EH wrote most of the manuscript with assistance from the co-authors.

III EH is the main author. Field experiments were planned and performed by the supervisors for several years before EH began work on this research. EH carried out field measurements and data analysis. Stand simulations were created by EH and Urban Nilsson. EH wrote most of the manuscript with assistance from the co-authors.

IV EH is the main author. Field experiments were planned and performed by the supervisors for several years before EH began work on this research. EH participated in the final field measurements. EH undertook the data analysis and wrote most of the manuscript with assistance from the co-authors.

Abbreviations

B	Treatments/stands with birch
DBH	Diameter at breast height
LDD	Long distance dispersal
MAI	Mean annual increcment
NFI	National forest inventory
NS	Treatments/stands with Norway spruce
NSB	Treatments/stands with Norway spruce and birch
PAI	Periodic annual increment
PCT	Precommercial thinning
SDD	Short distance dispersal

1 Introduction

1.1 The objectives of mixed forest

The effective use of forest products and appropriate management of land resources are both important for human welfare. Recently, forest policy and research have incorporated the concept of managing land use sustainable, including trade-offs between human needs and reducing the impact on other ecosystem services (Johansson & Keskitalo, 2014; Nordberg *et al.*, 2013; Foley *et al.*, 2005; Hooper *et al.*, 2005). Such changes in perspective have had an impact on management (Elbakidze *et al.*, 2013; Nordberg *et al.*, 2013). One example is the conversion from monoculture to mixed stands in management praxis in Europe (Bravo-Oviedo *et al.*, 2014b). Clearcut management systems, with high investment in regeneration measures, are often primarily about optimizing crop yield in monocultures. However, monocultures are unusual even in managed ecosystems (Harper, 1977), although weeding, tending, pre-commercial thinning (PCT) and plant improvement are costly attempts to take control over cultivation.

Clearcut operations have a negative impact on species biodiversity in boreal forests when compared to forests that were not subjected to past intensive forest management (Li *et al.*, 2009). Disturbance changes the field vegetation and severe disturbances can cause the extinction of shade-tolerant species adapted to mature forests (Aikens *et al.*, 2007), some of them with slow colonization rates (Brunet *et al.*, 2012). Replacing forests with no history of clearcutting with plantations result in reduced plant species richness (Bremer & Farley, 2010). Compensatory measures are invented and implemented to minimize the biodiversity losses, e.g. retention of living trees and dead standing trees and coarse woody debris, including retention of broadleaves in conifer stands (Fedrowitz *et al.*, 2014; Kruys *et al.*, 2013; Gustafsson *et al.*, 2012; Lindenmayer *et al.*, 2012; Abrahamsson *et al.*, 2009; Hazell & Gustafsson, 1999).

In addition to considerations at final felling, the inclusion of even-aged admixtures of broadleaves in coniferous plantations is also used as a strategy to increase ecosystem value (Bravo-Oviedo *et al.*, 2014b; Man & Greenway, 2013; Knoke *et al.*, 2008; Carnus *et al.*, 2006; Agestam *et al.*, 2005). There are some proven benefits, such as improved soil quality and increased biodiversity for specific taxa (Chauvat *et al.*, 2011; Felton *et al.*, 2011; Hansson *et al.*, 2011; Felton *et al.*, 2010; Ammer *et al.*, 2006). Forest stands where there are objectives other than wood production, such as erosion control or land rehabilitation, might be more effective as polycultures (Richards *et al.*, 2010). Coniferous stands with admixtures of broadleaves are more highly rated in studies of recreation and aesthetics than monocultures in Fennoscandia (Gundersen & Frivold, 2008). Diversity of forest products other than wood is enhanced by a greater tree species diversity in the boreal forests, including bilberries and mushrooms, the abundance of which could be correlated to tree species or specific habitats (Hedwall *et al.*, 2013; Pilz & Molina, 2002). One of the most discussed services associated with mixed forest is a general risk reduction (Bravo-Oviedo *et al.*, 2014a; Griess & Knoke, 2011; Jactel *et al.*, 2009), where the functional features of tree species exhibit different resilience with respect to disturbance agents, both abiotic, such as wind damage (Valinger & Fridman, 2011) and biotic (Li *et al.*, 2012; Jactel *et al.*, 2009). A reduction in the impact of pest and pathogen outbreaks in more diverse stands is achieved if dilution limits access to the targeted species (Conner *et al.*, 2014; Setiawan *et al.*, 2014) or when the more diverse biotope hosts natural enemies of the damaging agent (Jactel *et al.*, 2005). The obvious exception is when the pathogen needs alternating hosts (Mattila, 2005). In this case a specific mixture could be devastating.

1.2 Growth and yield

The ecological effect of mixed forests has been widely debated, sometimes resulting in contradictory conclusions. In many cases the confusion stems from researchers addressing different issues, and as a result adopting different spatial and temporal perspectives; e.g. evaluating ecosystem productivity versus stand growth and yield. This thesis addresses the latter issue, focusing on stand establishment and the early management of mixed forest.

Growth and yield of a crop could be regarded as a function of resource supply, acquisition and resource-use efficiency, and understanding mixtures requires a knowledge of how interspecies relationships affect these variables (Richards *et al.*, 2010). Density stress issues are fundamental when evaluating the plasticity of individuals, both with respect to productivity and sustainability e.g. planting densities or PCT treatments in Norway spruce *(Picea abies* Karst), or monocultures that explore the reciprocal law of yield and density (Nilsson, 1994; Pettersson, 1993). In monocultures, the weaker individuals grow less when exposed to competition and the dominant individuals maintain or even increase their advantage (Harper, 1977). In general, the same principle is applicable for mixtures and interspecies relationships; if one species is a weak competitor, it will be suppressed by the other species, and an additional supply of resources often enhances the advantage of the dominant species (Harper, 1977). However, sometimes an increase in a limited resource can change competition premises (Pretzsch, 2005), e.g. the higher stem volume growth of Scots pine *(Pinus sylvestris)* on poor soils compared to Norway spruce (Jonsson, 2001) that does not necessarily occur on fertile sites (Lindén & Agestam, 2003).

The perceived reduction in density stress in mixtures, is usually explained by complementarity between species, where one species facilitates the growth of other species, or as a sampling effect (Fridley, 2001). The exploitation of resources could be complementary in heterogeneous stands, i.e. the species occupy different strata of the resources available and generate an increased yield (Richards *et al.*, 2010). When interspecific competition is lower than intraspecific competition is therefore called a complementary effect (Kelty, 2006; Kelty & Cameron, 1995; Hamilton, 1994). A positive response to a species mixture could be that one species facilitates the conditions for the other, often an increase in resources in the ground (Laganière *et al.*, 2015; Schmidt *et al.*, 2015), e.g. by nitrogen fixation (Rothe & Binkley, 2001). However, though facilitation has sometimes been proven for specific combinations of tree species, there is no empirical proven general effect simply associated with increasing species diversity (Fridley, 2001; Rothe & Binkley, 2001).

Complementarity implies a diversification of the utilization gradient of nutrients, water and light. This could be the case spatially (Radosevich *et al.*, 2006), if the tree species in a stand exploit different soil depths for rooting, or temporally, in mixes of evergreens and deciduous trees using different resources across the seasons (Kelty, 1992). A decreasing stand yield in a mixture compared to the best monoculture sometimes occurs in boreal and temperate forests (Dirnberger & Sterba, 2014; Hynynen *et al.*, 2011; Jacob *et al.*, 2010; Knoke *et al.*, 2008). One explanation for this could be a rather low rate of differentiation between functional groups in these woody ecosystems due to species reduction during ice ages (Pretzsch, 2009). However, a complementary effect has sometimes been detected even for species with similar growth patterns and ecological traits (Collet *et al.*, 2014; Lindén & Agestam, 2003).

In many cases, a mixture is evaluated based on how the merchantable crop is affected by weeds and unwanted competitors. This is especially true for agricultural studies. When evaluating weed impact, an *additive* design is often chosen. The species have the same density in mixture treatments as in monoculture treatments so the design compares not only the effect of species characteristics but also an effect of increased density and density stress. A *substitutive* design (also called a replacement design) in an experiment is preferable when the stratification effect on resource utilization is of interest. The density is kept constant in the treatments, only species mixture and composition is varied (Harper, 1977).

Relative yield of a species is defined as the ratio of the yield in a particular mixture and the yield in a pure stand. The relative yield total (RYT) is the sum of the two species' relative yield (Harper, 1977). This is based on the reciprocal law of total yield being a response to plant density and individual plant growth (Shinozaki & Kira, 1956). If RYT in the mixture becomes higher than the expected sum of the yield of either one of the monocultures it is defined as overyielding; the opposite situation is known as underyielding. When the mixture produces more compared to both species this is known as transgressive overyielding (Pretzsch, 2009). In both additive and substitutive designs RYT can be tested, but RYT should be used as an indicator of mixture effects, not as a quantifier (Hamilton, 1994). Figure 1 shows an example of plotting the RYT for one of the simulations in paper III. Total volume production of the experimental plots after simulated PCT in three alternatives - Norway spruce monoculture, birch monoculture and a mixture of 80 % Norway spruce and 20% birch in the final stand -, provides a visual representation of the concept of evaluating RYT. In this case, the Mixed PCT alternative had an estimated production that was close to the theoretical production without any mixing effect (neither under- nor over- yielding).

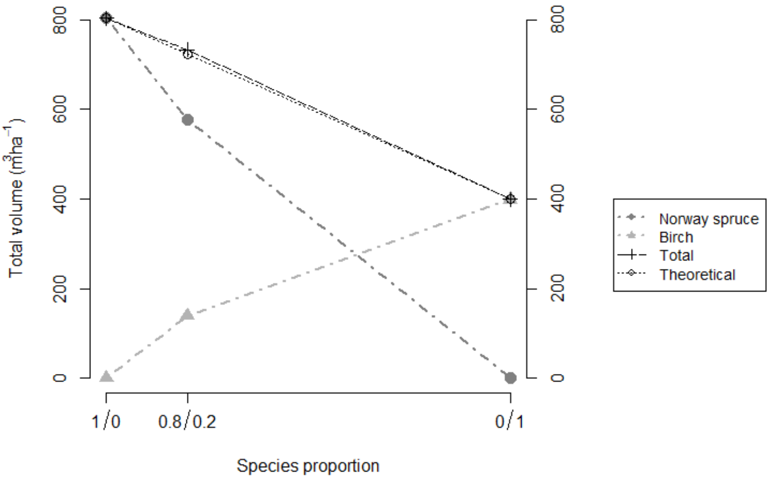

Figure 1. Total volume production (m^3 ha^{-1})of the two species in monocultures and mixture of 20% birch, 80 % Norway spruce. Species proportions on the x-axis, from left to right Norway spruce:100, 20 and 0 % and birch 0, 20 and 100 %. Also included in the figure, the Total production of both species and the Theoretical line representing no mixture effect.

Substitutive designs can answer the question of biological complementarity, whether the species might use different strategies when subjected to density stress. One example is how shade-tolerant and pioneer species could utilize different levels of the canopy when they need to increase leaf area (Man & Greenway, 2013). Sometimes overyielding has been demonstrated in this type of experiment (Bielak *et al.*, 2014; Pretzsch, 2009). However, the question of overyielding becomes out of context if not all species are mutually relevant as crop trees. Additive designs answer more specifically the question of whether the yield of one species is the same regardless of the presence of other species (Hamilton, 1994). In a conversion from a monoculture of one crop species to a mixed forest this approach is more relevant when testing yield against, or together with, other ecosystem services.

In even-aged monocultures, the use of light and soil resources will be similar for all trees (Kelty, 1992), compared to mixtures, where the variation will be greater (Morin *et al.*, 2011; Larson, 1992). In experiments, comparisons are made for the total stand/population or the individuals within the stand, examining how they are affected by their neighbors (Dirnberger & Sterba, 2014; Porte & Bartelink, 2002). An alternative to expensive stand experiments is individual tree-analysis (Kelty, 2006). Studying how the plasticity of plants responds to interactions between density and resource limitation provides information when comparing inter- and intraspecific relationships. Important factors to consider are the number of neighbors and plant size, both within a given timescale and in relation to other neighbors. In mixtures, the species and/or functional groups of species are added to the variables of importance. Yield experiments involving mixtures are usually based on different grid designs, with species frequency and proportions as treatments. The density needs to be at a sufficiently high level to ensure competition. It is possible to combine the population and plant evaluations if the spatial pattern of the planted trees is appropriate for both (Kelty & Cameron, 1995).

Understanding productivity differences between monocultures and mixtures of species is the main purpose of many experiments. Traditionally, experiments have been restricted to less than one rotation period and the outcome is the total value from this period. Within this timeframe, the stand structure varies in density and proportions, but usually does not involve more than two species. In addition, the comparison between monocultures and mixed stands may not produce the same result for total yield during a whole rotation as for yield in the middle of a rotation (Fahlvik *et al.*, 2011).

Experiments examining species interactions are expensive to perform on a stand scale and/or over the long term (Kelty, 2006). To extrapolate from small scale experiments, the results are often combined with modeling of growth. With models, it is also possible to combine survey data from national forest inventories (NFI) containing data from a large area, with data from experiments with controlled treatments. The NFI data could also serve to validate models. Recent studies on NFI material correlated productivity, in terms of tree biomass production, with tree species diversity (Gamfeldt *et al.*, 2013; Vila *et al.*, 2007). However, using survey data to state causal effect of one variable of the other(s) is not possible; the data can simply test correlations. On the stand scale level, when the objective is to evaluate production capacity in relation to species richness, tests must be conducted within a controlled range of specific abiotic conditions for which there may be interactions (Man & Greenway, 2013; Hooper *et al.*, 2005). The natural variation in the abiotic conditions that affect density stress, resource deficiency and thus species’ functional differences in productivity have to be considered in such comparisons, e.g. soil fertility (Mielikäinen, 1994). This variation in resources, combined with a range of species mixtures, is difficult to find in natural systems (Hooper *et al.*, 2005). Furthermore, species identity and species composition explain more than a general variable of species richness (Laganière *et al.*, 2015; Nadrowski *et al.*, 2010). Using survey data at such a large scale, as NFI data, highlights a third possible effect of growth and yield in mixtures, referred to as the sampling effect (Fridley, 2001). By increasing the number of species, the likelihood to of adding high yielding species also increases, as well as combinations of species which have complementary or facilitative effects (Morin *et al.*, 2011). The sampling effect is one of the elements which affects species' composition in ecosystems. On a regional or global scale, the biodiversity and large species pool are the fundamental premises for potential high production (Hooper *et al.*, 2005; Fridley, 2001).

1.3 Definitions and descriptions

The relatively small number of existing European forest experiments involving mixed stands (Agestam *et al.*, 2005) could justify the use of robust models and informatics constructed for the species in monocultures. Testing model predictions in long-term experiments (Hynynen *et al.*, 2011; Mielikäinen, 1985) showed no bias based on the birch admixture percentage, even though the model may slightly underestimate the total volume (Hynynen pers.com 2015). Two important examples of outputs of Swedish forest research are the national spatial coverage of forest data on species and standing volume, k-NN Sweden, and the stand and landscape simulator Heureka, both partly based on NFI data.

The sampling design of the Swedish NFI was chosen to provide accurate values of total standing volume at a regional level, on a resolution of 25000 ha. This is sufficient for the original purpose of the survey, to monitor status and changes on a regional scale. The data are designed to facilitate the calculation of five-year estimates for the forests in all the counties in Sweden. Combining satellite raster data with the field-measured sample plots with interpolation increases the resolution and decreases the residual mean square error (RSME). The interpolation method chosen for Sweden is a probability-based k-nearest neighbor technique (k-NN Sweden) (Reese *et al.*, 2003; Reese *et al.*, 2002) and it is often used when multiple continuous attributes need to be estimated (Brosofske *et al.*, 2014; Gilichinsky *et al.*, 2012; Tomppo *et al.*, 2008). k-NN Sweden is available for three time periods, based on the 5 year interval of the NFI data: 2000, 2005 and 2010.

The stand and landscape simulator Heureka is a framework of models for all stages in the forest management cycle. The models are based both on individual trees and whole stands (Fahlvik *et al.*, 2014; Wikström *et al.*, 2011; Elfving, 2010). Within Heureka, it is possible to combine species-specific growth functions and species' responses to management, such as PCT and thinning. The functions are mostly derived from NFI data, but other data sources are also represented such as long term experiments, measurements of felled sample trees and permanent sample plots (Elfving, 2010; Söderberg, 1986; Agestam, 1985).

Guidance in forest management is often provided only for monocultures and this lack of general knowledge could perhaps be one reason for the reluctance to shift to mixed forests in practice (Bravo-Oviedo *et al.*, 2014a). In Fennoscandia, species-specific growth models have been tested for species in mixtures with good results (Agestam, 1985). However, resilient forest management, to provide robust protection of the ecological system (Kerkhoff & Enquist, 2007), may require other research hypothesis than comparing the least comparable units between poly and monocultures. It may be difficult to manage a mixed forest sustainably over time when only one or two of the tree species account for the timber value (Kelty *et al.*, 2011). For example, the thinning guides used in Swedish forestry are based on basal area (density), height and site fertility (resource availability) and aim to optimize harvestable yield for the target species. Adding another species implies the addition of several other variables. Not only the new species density stress as a function of resources, but also the proportion of the two species and eventual facilitation or complementary use of resources needs to be incorporated. As an example, for birch the recommended stem density in mature stands is much lower than for Norway spruce (Hynynen *et al.*, 2010). However, the multiple objectives that may be behind choosing mixed stands motivates also different thinning regimes, stand rotation lengths and intensity so that optimization will differ from that based on pure productivity goals.

There are many definitions of what a mixed species forest really means. The term often needs to be accompanied by some declaration of purpose and a description of the relevant context (Bravo-Oviedo *et al.*, 2014b) but this definition is sometimes used and could be valuable (Olsthoorn, 1999): *"…stands composed of different tree species, mixed on a small scale, leading to competition between trees of different species as a main factor influencing growth and management*'. This very broad definition may be superior to more restricted ones that apply to specific situations but needs to be further limited for relevant understanding and use. Such specific definitions may include a variety of aspects. First, number of species and their proportions, described in terms of stem density, basal area, volume etc. Secondly, the vertical structure of the forest, age or height differences or numbers of layers in the canopy.

Third, the spatial structure of the mixture, indicating whether the tree species are in clusters or rows or if the trees are individually mixed. In addition, the temporal aspect of stand development needs to be considered. Often the mixed species structure in a forest is temporary. It could be the result of the transition from a stand dominated by pioneers to the establishment of shade tolerant species as the forest matures, or a shelterwood of one species protecting another planted species (Prevost & Dumais, 2014; Man *et al.*, 2010).

The definition of mixed forests used in national statistics varies between countries. In Sweden a mature forest containing conifer and broadleaved species is defined as being ‘mixed’ when a maximum of 65% of the basal area consists of one the dominant species (*Skogsdata*, 2014). In Norway the same limit is 80% of the basal area of the species (Johansson, 2003) and in Finland 75 % (*Finnish statistical yearbook of forestry*, 2014). Often even-aged mixtures are established by planting the preferred commercial species and allowing spontaneous natural regeneration of other species present at the location. In most cases, the planted species will be a conifer, for example the native Norway spruce or Scots pine, but sometimes exotics as lodgepole pine (*Pinus contorta)* or hybrid larch (*Larix x eurolepis)*. In southern Sweden, planting mixtures is rather unusual but does occur, especially on former agricultural land. (Johansson, 2003).

1.4 Mixed forest of birch and Norway spruce

Managing coniferous forests in Fennoscandia has traditionally involved dealing with the spontaneous regeneration of other tree species by means of both preventive and reactive measures (Johansson, 2008; Björse & Bradshaw, 1998). This was mainly because, historically, the broadleaved tree species’ were of limited economic value and most species also produced biomass more slowly than the native conifers. Herbicide treatments to reduce competition from woody species have been prohibited on forest land since the early 1980s. Since then PCT has been the standard way to remove trees that compete with the crop trees. The most abundant naturally regenerated broadleaved tree species on clearcuts in southern Sweden are the two native birch species: silver birch (*Betula pendula* Roth) and downy birch (*Betula pubescens* Ehrh) (Götmark *et al.*, 2005). In this thesis, these two species are both referred to as birch and are not differentiated unless specified. Other frequent naturally regenerated broadleaves are aspen (*Populus tremula* L), rowan (*Sorbus aucuparia* L), goat willow (*Salix caprea* L), black alder (*Alnus glutinosa* L Gaertner) and oak (*Quercus robur* L).

Birch is the most important broadleaved tree species in northern Europe (Hynynen *et al.*, 2010) and mechanized techniques for harvesting small-dimension wood have been developed (Ulvcrona *et al.*, 2013; Bergström *et al.*, 2012; Bergström *et al.*, 2010). The demand for hardwoods as bioenergy and cellulose product are perhaps, the main markets for birch in these dimensions. In addition, the practice of using birch as a shelter for improving survival and quality in young plantations of Norway spruce has become more accepted, as has managing young conifer stands as mixtures in general.

As mentioned previously, a species mixture with two species that complement each other with respect to different functional traits probably has additional positive effects on biodiversity (Korner, 2005). The combination of Norway spruce and birch is a good example of species with many contrasting functional traits, e.g. evergreen conifer versus deciduous broadleaf (Felton *et al.*, 2015 In press; Johansson, 2003). Birch, in contrast to Norway spruce, is a pioneer tree species, which implies fast establishment on disturbed soils and rapid initial growth (Franceschini & Schneider, 2014).

Another incentive to increase the area of mixed forest is certification. Forest owners can quantify and certify their forest as being sustainably managed by achieving standards from for example, FSC (Swedish FSC Standard for Forest Certification including SLIMF indicators, 2010). Almost 50 % of the productive forest in Sweden was certified in 2012 (Johansson & Keskitalo, 2014) although the accountability associated with the Swedish standards has been questioned somewhat by non-governmental organizations (Johansson, 2012). In current Swedish certifications, including broadleaved species in coniferous mature stands is one of the requirements (§6.3.8 FSC standard; 10 % of the standing volume in southern and 5 % in northern Sweden).

Despite the objectives and demands for the mixed forests of Norway spruce and birch that are often cited, the management in the clearcut phase is not explicitly adapted to deliver this final goal for the stand. The question is whether operations undertaken during a traditional clearcut of a Norway spruce stand are sufficient for the establishment of a mixed forest. The combination of planting Norway spruce and allowing birch to regenerate naturally might, if successful, be no more costly than the monoculture. In fact it can be less expensive in many cases. Furthermore, if spontaneous regeneration of additional species occurs, even though in small proportions, there is an opportunity for the forest owner to increase biodiversity value as well as achieving economic goals.

1.5 Birch management in Norway spruce plantations

The regeneration ecology of the two native birch species is relatively well studied and described in forest literature (Hynynen *et al.*, 2010; Karlsson, 2001; Perala & Alm, 1990a; Perala & Alm, 1990b; Sarvas, 1948; Lappi Seppälä, 1947). The species are similar in their phenology and traits (Eerikäinen *et al.*, 2007) and seldom separated in Swedish forestry practice or in the Swedish national forest inventory (NFI). Downy birch has a larger spatial distribution in altitude (Holm, 1994) and is more abundant in the northern part of Sweden, it also flowers later in spring and produces a slightly lower proportion of viable seeds (Sarvas, 1952). In southern Sweden silver birch seedlings seems to be more frequently found on clearcuts, as to the opposite in northern parts of the country. This is however, difficult to find scientifically stated, especially since the Swedish NFI does not separate the two species. The shift of abundancy between the species along the latitudinal gradient has been detected also in Finland (Sarvas, 1948). The growth and vitality of silver birch tend to respond more to differences in soil properties and it could be sensitive to flooding, compacted soils and infertile sites (Hynynen *et al.*, 2010).

To control or predict how a species reproduces and disperses includes the knowledge of several variables associated with seed supply and seedling emergence (Agestam *et al.*, 2005; Karlsson, 2001). In this context, some variables serve as mean differences between species, such as the seed weight of silver birch and downy birch (Sarvas, 1948), others represent tipping points, such as the wind strength required for seed abscission (Schippers & Jongejans, 2005) whilst, others can be considered oscillating functions, such as the proportion of viable seeds affected by annual climate (Sarvas, 1952). Birch has a high dispersal potential and exhibits some of the common features for such tree species: short juvenile period, low seed mass and short intervals between years with high seed production (Rejmanek & Richardson, 1996). Potentially, birch can start to reproduce at 10-15 years (Perala & Alm, 1990b). The size of the individual crown is the strongest trait affecting seed production (Fenner, 2005; Sarvas, 1948) and consequently a solitary tree produces more seeds than a tree subjected to competition in a forest stand. Instead of crown size, basal area or standing volume are correlated traits used as stand estimates of potential seed production (Greene & Johnson, 1994). The wind-spread seed can be described with short or long distance dispersal distributions (SDD and LDD), depending on purpose of the model (Bullock *et al.*, 2006; Nathan & Muller-Landau, 2000). The vast majority of birch seeds fall to the ground within 100 m from the source (Karlsson, 2001; Fries, 1984). SDD modeling is mainly used when considering the dispersal from a single specific source to a specific site with a targeted density of the new stand in mind. However, the LDD has been reevaluated and upgraded in dispersal theory, since it explains migration of species in general, adaptation to habitat changes and also the landscape probability or presence of a seed supply (Fenner, 2005; Nathan & Muller-Landau, 2000).

To secure sufficient seed supply, the distance to the seed source is, of course, of major importance. The size of the clearcut and its distance to adjacent stands or the retention of vital seed trees are the two possible variables to consider to ensure seed supply (Fries, 1984). Removal of slash residues for bioenergy purposes also facilitates seed germination by increasing the chance that seeds will land directly on the forest soil (Karlsson *et al.*, 2002).

Several variables are important at the microsite where the seeds land. Seedling emergence and survival are dependent on for example the right soil moisture content (Oleskog *et al.*, 2000; Frivold, 1986), site fertility type (Lehtosalo *et al.*, 2010) and shelter wood (Karlsson & Nilsson, 2005). Microsite conditions can be manipulated by soil scarification techniques, already used in traditional clearcut management. Soil scarification is beneficial for natural regeneration in general (Clark *et al.*, 2007; Newmaster *et al.*, 2007; Karlsson & Nilsson, 2005), and for birch specifically (Nilsson *et al.*, 2002). Seedlings that emerge on bare mineral soil have a greater chance of survival due to the favorable microclimate and reduced competition. Soil scarification combined with conifer planting is the most common regeneration method, on more than 80 % of Swedish clearcut areas (*Swedish statistical yearbook of forestry*, 2014). Important purposes of soil scarification are to prevent pine weevil damage on the planted conifer (Wallertz & Petersson, 2011; Petersson *et al.*, 2005) and to reduce competition from ground vegetation (Löf *et al.*, 2012). Soil scarification has both a short-term positive effect on survival of the planted material (Johansson *et al.*, 2013b) and a long-term effect on growth and stand production (Johansson *et al.*, 2013a).

A few years after regeneration, the density of naturally regenerated seedlings on a clearcut in southern Sweden could be higher than the planted seedlings. (Nilsson *et al.*, 2002). PCT is almost entirely motivated by the desire to reduce competition affecting the preferred conifer crop trees and to select future crop trees (Weiskittel *et al.*, 2011; Wagner, 2008; Pettersson, 1993). However, many forest owners also intend to create a mixed stand in the present regeneration (Fällman, 2005). PCT is performed manually with brush saws when the saplings reach between 3 and 5 m. Cut stems are retained on the site because income from small dimension birch is normally lower than the costs of harvesting. Both birch species respond by sprouting when cut as a seedling or a sapling (Kauppi *et al.*, 1991; Andersson, 1985). Sprouting from birch stumps is often considered to negatively impact the crop trees (Hynynen *et al.*, 2010; Johansson, 2008; Walfridsson, 1976) and is one reason why the timing of PCT is often discussed. A delayed PCT may reduce the effect from sprouting stumps. On the other hand, an early PCT enables early selection of future crop trees and thereby stand composition and is less expensive. Possible alternative methods for same purposes, used in countries with similar forest management systems, could be an early tending when crop seedlings reach about 1 m height and thereafter PCT at 3-5 m height, common in Finland, or herbicide treatments or combinations of herbicides and PCT (Bataineh *et al.*, 2013)

The well-known strategy of using birch shelter to protect Norway spruce saplings is a good example of a stratified mixture employing different horizontal levels of the canopy for each species (Kelty, 2006). However, the stratified structure changes when the Norway spruce overgrows the birch and often the stand will be thinned and managed as a Norway spruce monoculture after canopy closure (Lindén, 2003).

1.6 Experiments with birch and Norway spruce

Even though experiments with native species are most common as monocultures, the early management of birch and Norway spruce mixtures is one of the most studied polycultures in Fennoscandian field research. In such experimental work, two main objectives are often found, not unusually in combination: to estimate the production capacity of the species, and to test the resilience of the mixture through time and as the stand develops. Experiments or field surveys are often evaluated based on measures of periodic annual increment (PAI) of both species or individual species, for the total stand or only for main stems/crop trees. Another option is to use mean annual increment (MAI) over time and during stand development. The growth patterns of the two species are rather different, so the comparable unit of different stand compositions benefits from optimization of the stand rotation length based on timing of maximum MAI.

Often the structure or composition in the mixture is the relevant difference between studies. The relationships between species competition and height differences in young stands have major importance for conclusions about both vitality and yield (Fahlvik *et al.*, 2005). In single-storied experimental plots, mixtures have lower total production than pure Norway spruce plots with same total density (Fahlvik *et al.*, 2011). When both species are naturally regenerated, the stand is often two-storied in the early years. The birch grows as a shelter over the Norway spruce seedlings and several studies have demonstrated an equivalent or increased yield in mixtures as in Norway spruce monocultures (Lundqvist *et al.*, 2014; Fahlvik *et al.*, 2011; Agestam *et al.*, 2005; Bergqvist, 1999; Mard, 1996; Tham, 1994). One long-term experiment showed that the positive effect of the mixture declined as the stand grew older (Frivold & Frank, 2002). However, the study also emphasized that the birch shelter probably had a low competitive impact on Norway spruce since mortality in the experiments was low. Other studies have focused on the facilitation effect of the birch shelter on planted seedlings (Langvall & Ottosson Löfvenius, 2002; Klang & Eko, 1999) and have explained the effect as resulting from the reduced risk of frost damage. It is possible to manage the birch shelter for increased profitability even though management of the two layered stand is probably more labor intensive (Valkonen & Valsta, 2001).

Besides the yield estimates, other management implications of growing mixtures are of interest. The risk of whipping damage to Norway spruce from birch has been studied and the conclusion is that there is probably little effect on the final crop (Fahlvik *et al.*, 2011; Lindén, 2003). The well-known sprouting behavior of birch when the saplings are cut (Kauppi *et al.*, 1991) has also been the subject of management studies (Hynynen *et al.*, 2010; Andersson, 1985). During the first years after PCT, the sprouts will grow faster than other birch saplings (Kauppi *et al.*, 1988) and the sprouting response after PCT may be rather apparent (Johansson, 2008; Andersson & Björkdahl, 1984).

1.7 Browsing impact

Damage to seedlings and saplings from ungulate browsing is a well-known complication in Swedish forestry (Bergqvist *et al.*, 2014; Valinger *et al.*, 2014; Bergqvist *et al.*, 2001). For some broadleaves, there are government subsidies for fencing but this is not the case for birch or conifer regeneration. The ungulate populations and their preferences for different species (van Beest *et al.*, 2010) have an impact on future stand composition (Speed *et al.*, 2013; Elie *et al.*, 2009; Casabon & Pothier, 2007). Aspen, pine and birch are more attractive to moose (*Alces alces*) than Norway spruce (Jalkanen, 2001; Kullberg & Bergstrom, 2001). In mixed stands, where attractive species are included, browsing damage could be more severe (Milligan & Koricheva, 2013; Vehviläinen & Koricheva, 2006). However, not only the stand but also the species composition in the surrounding landscape will have an impact on the browsing pressure on individual seedlings (Herfindal *et al.*, 2015; Bergman *et al.*, 2005; Edenius *et al.*, 2002; Hornberg, 2001). With an increased forested area of a less preferred species, such as Norway spruce, the browsing pressure will increase on stands with preferred species, such as pine or mixtures containing broadleaves (Kalen, 2005).

2 Objectives

The overall objectives of this thesis all refer to the establishment and early growth of managed forest stands with planted Norway spruce and naturally regenerated birch. More specifically the objectives were:

To test whether spatial information about the location and standing volume of birch trees in the landscape can be used to estimate seed sources to allow improvements in site-specific predictions of natural regeneration of birch on clearcuts (Papers I and II).

To evaluate whether traditional regeneration treatments in Norway spruce plantations in southern Sweden are sufficient to establish mixed forests, including planted Norway spruce and natural regeneration of birch and other less frequent tree species (Papers II and III).

To evaluate whether mixtures are sustainable over the whole rotation with current planting densities or if a substitutive design with a reduced density of planted Norway spruce is necessary to keep the birch viable when competition increases in the older stand (Papers III and IV).

To evaluate how pre-commercial thinning in dense regenerations may enhance survival and growth of both species, considering timing and intensity, species composition and height differences between species (Papers III and IV).

3 Methods and modeling

Two regeneration experiments were used as the basis for the analysis in papers I, II and III, and one PCT experiment was the basis for the analysis in paper IV. The experiments were replicated in blocks which were in total distributed in five areas, according to Figure 2. All the experiments had objectives associated with managing mixed Norway spruce and birch stands. Almost all blocks were established on sites that were harvested in conjunction with storm Gudrun in 2005, which affected southern Sweden in the region of Kronoberg county in Småland and Halland.

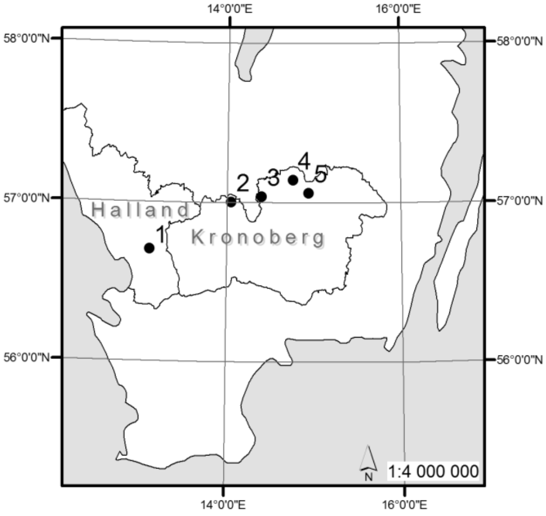

Figure 2. Map of Southern Sweden with numbered areas associated with the field experiments included in the thesis.
1: papers I,II,IV, 2: paper IV, 3: papers I-III, 4: papers I-III, 5: paper IV.

Both regeneration experiments were randomized block designs located on six different sites in three areas. They were designed to be future long-term experiments with treatments relevant to managing mixed species forest over the full stand rotation. All sites were on mesic, till soils and the previous stands were dominated by Norway spruce. Site fertility was medium to high for the region. One of the experiments used two techniques of soil scarification for the soil disturbance treatments, separately or combined, disc trenching and inverse scarification (see example in Figure 3). The other experiments had two levels of soil disturbance, disc trenching or no active soil scarification. However, since all sites originated from severe storm damage clearcuts, even the sites with no active soil treatment were disturbed, after the uprooting caused by the storm and then the disturbance caused by logging machinery. In addition, treatments with different planting intensities were implemented, with levels of 0, 1500 and 2800 Norway spruce seedlings ha^{-1} in the first, and 0 and 2800 seedlings ha^{-1} in the second experiment.

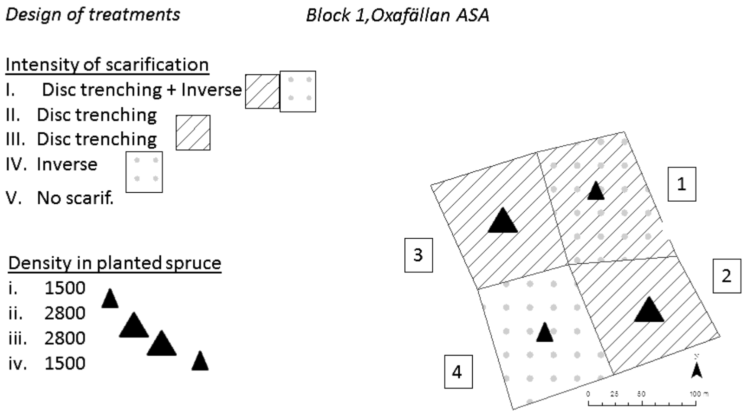

Figure 3. Example of design and distribution of treatments, Block 1. site Oxafällan, area 4.

Five years after harvest, the regeneration of seedlings (<1.3 m) and saplings (>1.3 m) of all tree species and height classes were measured in sample plots. The circular sample plots, radius 1 m, were distributed in a quadratic grid over all blocks and treatments with grid size either 5*5 m or 10*10 m depending on treatment plot size (0.1 ha or 1.0 ha). In total, 2061 sample plots were examined over 20 ha of experimental plots. The inventory data from these experiments were used as validation data in paper I, for model testing in paper II and as starting values for simulations in paper III. Treatments in detail are presented in papers II and III.

Modeling the dispersal of seeds from source to a clearcut can be approached in different ways. Theoretical modeling of wind turbulence and seed transport and empirical measurements of seed fall could be used in combination or separately (Canham & Uriarte, 2006; Karlsson, 2001; Greene & Johnson, 1996; Greene & Johnson, 1989; Fries, 1984). Papers I and II include models of how seedling establishment depends on seed dispersal and clearcut management. In paper I, the prediction itself for a specific chosen site, represents the core of the study, while paper II aims for a more general exploration of how the treatments and biotic covariates interact.

Paper I was based on a framework model, combining possible seed supply with seed emergence and survival based on GIS data and information from earlier experiments (Figure 4). The spatial distribution of seeds available in the landscape, called seed shadows, was calculated for the clearcut and surroundings in the form of raster data sets. The seed shadows were determined by combining the spatial data pertaining to standing volume in forests (k-NN Sweden 2000, 2005 and 2010), empirical knowledge of birch seed production in mature trees (Sarvas, 1952; Sarvas, 1948) and birch seed dispersal distributions. Two different ways to estimate dispersal were compared, one based on knowledge of wind turbulence and seed dispersal on a clearcut (Greene & Johnson, 1996) and the other based on an experiment with seed traps (Waelder *et al.*, 2009; Karlsson, 2001; Stoyan & Wagner, 2001). Of the possible seeds landing on the clearcut, the probability of germination and survival as a seedling was modeled in relation to soil moisture conditions and soil scarification. The empirical basis for the latter part was earlier experiments conducted in southern Sweden.

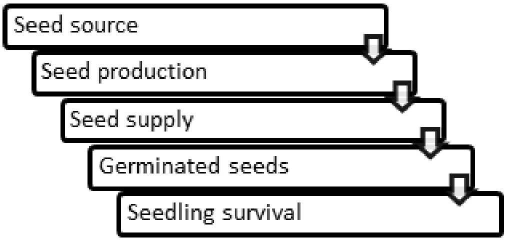

Figure 4. Flowchart summarizing the model of birch seed supply and seedling regeneration.

In papers III and IV, growth responses of young established stands were investigated, using stand density, species proportions and height variation of saplings. In both papers, management by PCT was initiated for setting treatment levels and to induce the growth response.

Paper III described simulated PCT treatments for the sapling data from one of the experiments used in paper II. The simulations aimed at mimicking the scenario of manual selection of retention stems in a PCT. The selections were made by prioritizing differently in five simulations including three mixtures of Norway spruce and birch and the two species in monocultures. The simulations were conducted based on two initial planting density treatments and all simulations had the same goal for stand density after PCT, 2000 stems ha^{-1}. Remained density but different approaches of birch retention, made it suitable to evaluate the possibility of influencing stand development with PCT selections. The modeled stands were further developed over 100 years using the Heureka modeling system. The study evaluated both the mean annual increment (MAI) and the likelihood of success in retaining the two species mixture during a full stand rotation. The predictions for several decades ahead were constructed using the empirical data of establishment success, PCT objectives in simulations and the known stand behaviors of Norway spruce and birch. In addition, one simulation was run with the aim of maximizing the total number of species of all regenerated seedlings in the stand, a multiple species approach. This was conducted to evaluate the potential for adding more tree species to the mixture.

In paper IV, empirical data was used to test the effect of PCT on growth response for retained Norway spruce and birch trees. The treatments included were designed with both additive and substitutive levels of birch and Norway spruce competition. The PCT experiment involving mixed regeneration of Norway spruce and birch was established on 11 sites in three areas around latitude 56-57 N, (figure 2). The sites were selected for their homogenous mixtures and relative heights of the species. The sites varied in initial heights of the Norway spruce, between 1 and 5 m. The initial heights were classified in three stages of the timing for PCT treatment. Main stems were selected and measured for height, dbh (diameter at breast height 1.3 m) and damage at the time of the PCT treatment and three and five years after PCT. The treatments were retention of 1000 or 2000 stems ha^{-1} of Norway spruce, with no birch or birch at 1000 stems ha^{-1}. Treatments were replicated with and without annual removal of birch stump sprouts. The periodic annual increment (PAI) over five years was calculated for total stand volume and individual trees, both mean values of all retained stems and the initial dominant trees. Further details of the experimental setup can be found in paper IV.

4 Main results and discussion

4.1 Regeneration

It is possible to predict birch seedling densities on a fresh clearcut (paper I). A series of functions for seed production, seed dispersal, seed germination and seedling survival was combined in a framework model (Figure 4). The model predicts, with accuracy, whether the regeneration is sparse (0-1000 seedlings ha^{-1}), dense (>30000 seedlings ha^{-1}) or intermediate. Birch trees in the adjacent forest stands are the main suppliers of seeds to the clearcut and it is possible to model how the seed dispersal out of these stands behaves. Modeling seed dispersal with the theoretical equations for wind dispersed seeds or based on seed trap data gave similar levels of seeds when compared over a landscape. Using the estimated seed supply based on k-NN Sweden provided a better explanation of the birch seedling density compared to local mean (~80 ha) or county means (Halland or Kronoberg) of standing volume. The residual mean for estimated site density against measured data was smaller (-0.19) than the two general estimates, local mean (-0.31) and county mean (-0.37). The mean residual error of the model at the sample plot level was even smaller: 0.003. However, the variance was still large and many other variables could be implemented in the model framework to increase predictive certainty in the future.

Whereas in paper I the seed distribution was modeled for both short and long distance dispersal, only the short distance was considered in paper II. Here, the distance to seed source was an important variable to explain the abundance of birch seedlings but the two experiments was primary undertaken to test the effect of soil scarification treatments. The distance to seed source was used as a covariate to model the eventual seed limitations.

Soil scarification improved natural regeneration and the effect increased with the intensity of the soil disturbance. Birch was the most frequent tree species regardless of scarification type. On average 60 % (paper II) was birch, of which 15 % was downy birch. Birch densities varied between 500 and 17 000 seedlings ha^{-1} between blocks and treatments. In total, 11 native tree species were found naturally regenerated in the experiments but only Norway spruce, goat willow and aspen were found in all blocks, and none of them constituted more than 50% of the density in any block.

Even though the soil disturbance treatment produced significant effects, the variance within the same scarification type was rather high (paper II). Some of this variance was explained by the modeling of the seed supply (paper I). Both papers show the possibility for making predictions of potential birch regeneration, and the opportunity to influence future regeneration by choice of soil scarification. However, site fertility and soil moisture content are important site variables that could be further tested in order to expand the value and usability of the model. The sites chosen for these experiments were on medium- to high fertility, mesic soils in order to reduce potential interactions with seed-specific variables or management. At the randomly selected sites (paper I), the soil moisture class varied and therefore this variable was included in the model.

Using the mean stand density as a comparative unit for treatments or as a descriptive measure for regeneration success may be insufficient in natural regeneration. The variable abundance of seedlings, often in clusters (Eerikäinen *et al.*, 2007), is different from the even distribution of planted seedlings. Therefore, the treatment effect in the gridded sample plots was tested with a distribution describing the clustering behavior of seeds and seedlings and overdispersion of zero plots (paper II). About 50 % of the sample plots were without any birch seedlings, (actual zero plot or occupied by planted Norway spruce or naturally regenerated tree species other than birch). One reason for the high number of zero plots was the sampling design, with a tight grid of small sample plots. The design was chosen to capture the clustering behavior of the natural regeneration and the variability in treatment effect at the stand level. The treatment was a stand level operation, testing the scarification techniques and soil disturbance rates used in practical forestry, continuing the research on microclimate and soil bed substrates. The variables associated with vegetation cover and occupation served as complementary variables describing the effect of scarification techniques, where for example, disc trenching tends to pile up slash residues and thereby creates spots that are less suitable for seed germination, resulting in zero plots. The model showed the significant regeneration improvement with disc trenching but also its potential to give the appearance of regeneration into rows, if desired.

In some cases, the presence of zero plots was also because of limited seed supply. Using the distance to seed source as a covariate was also an important variable to consider in relation to the dispersal behavior of wind dispersed seeds. The effects of scarification were weak at distances greater than 60 m from the nearest potential seed source, indicating a change in the limiting variable affecting seedling recruitment (paper II). The seed supply was estimated solely from the minimum distance to a possible seed source, either a retention tree or a forest edge.

One conclusion from the findings presented in papers I and II is that studying short distance dispersal is primarily important on a stand level. However, long distance dispersal should not be neglected for the understanding of birch regeneration on a landscape level and may explain variation between sites. This conclusion and the results of the papers support data presented in earlier studies of both birch dispersal specifically (Karlsson, 2001; Fries, 1984) and theories of seed ecology in general (Stoyan & Wagner, 2001; Greene & Johnson, 1996; Greene & Johnson, 1995; Greene & Johnson, 1989).

The traditional management of a Norway spruce clearcut that was used in the experiments described in paper II included soil scarification, slash removal, occasional birch retention trees and clearcut sizes between 2 and 6 ha. At almost all experimental sites, no additional regeneration measures were needed to achieve stand level regeneration of birch. This indicates that the conventional methods used in planted conifer monocultures are, in general, suitable for the establishment of mixed forest comprising planted conifer and naturally regenerated birch.

4.2 Early management

Maintaining an even aged mixed stand through the full rotation is possible if the stand density and height development of the different species is considered during early management. The structure of the mixture was tested by selections during PCT, either by changes in the relative height of the species (paper III) or by varying the density (paper IV) or species composition (papers III and IV). In the PCT simulations (paper III) with variation in birch heights (keeping the tallest, keeping the best quality or keeping those with the same dimensions as the Norway spruce) the selections had little impact on MAI of the stands over a full rotation period. This could be partly explained by the competition from Norway spruce that affected all three alternatives. Most importantly, the simulation was based on measured data, and did not provide three different ranges of heights. Like a real PCT, the range of alternatives was limited to the seedlings on the site and in many cases the same seedling had to be retained for two or all three of the simulations. In the choice of sites for the experiment in paper IV, the height and diameter differences between the species were important. All sites had similar, single storied characteristics and eventual dominant birches were not chosen to be future main stems. The experiment was intended to test the density differences in single storied stands and in order to reduce other covariates, variation in height differences was minimized.

High and low densities of planted Norway spruce produced a different forest structure in the simulated mature forest. Only 10 % of the saplings after PCT simulations were birch in treatments with high density plantings (which is the recommended planting density in southern Sweden on sites with these fertility classes). At the end of the rotation period, the birch proportion of standing volume was 2-5 %, which is far below the current FSC standard requirement of a minimum of 10%.

In the low planting density treatments, the mean birch proportion was 30% of the saplings after simulated PCT and 18-21% of the standing volume at end of the rotation period. Of the five simulations, all remained as intended of the PCT, with two monocultures and three mixtures. The simulated maximum MAI was reduced by 1 m^3 ha^{-1} for the low planting density treatments compared to the high density. The total volume production and stand rotation length was lower in the mixtures compared to the Norway spruce monoculture for the low planting density treatments, but maximum MAI was very similar.

In the PCT experiment (paper IV), the total growth was higher for control plots compared to treatments if all seedlings regardless of tree species were accounted for. The mean seedling density before PCT was 10 000 seedlings ha^{-1} but on some sites the density was much higher, at most 48 000 seedlings ha^{-1}. All PCT treatments with annual removal of sprouts had a positive effect on growth of the main stems for both species compared to control plots. For the dominant individuals of Norway spruce, (the largest individuals before treatment, 1000 trees ha^{-1}) the mean MAI was small and in most cases non-significant between the treatments (Figure 5). There was no interaction between treatment and height classes for timing of PCT. No measured negative effect of birch competition was found on Norway spruce, but birch showed reduced growth with increased competition from Norway spruce. These findings were consistent with earlier findings, that density and neighbor size are more important than species identity (Barbeito *et al.*, 2014; Collet *et al.*, 2014; Li *et al.*, 2013; Lintunen & Kaitaniemi, 2010; Fahlvik *et al.*, 2005).

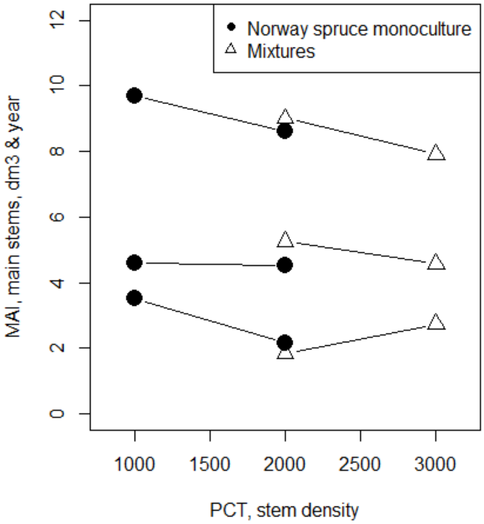

Figure 5. Mean MAI (dm^3 year^{-1}) for dominant stems of Norway spruce(NS) in PCT treatments, mean values for the blocks in height classes. Treatments in the figure: Circles: NS monoculture, 1000 & 2000 trees ha^{-1} Triangles: Mixtures, 1000 NS +1000 birch trees ha^{-1} & 2000 NS+1000 birch trees ha^{-1}.

In addition, early PCT, with mean initial heights of 1 m, resulted in a positive response to treatment and no significant interaction between initial heights and treatments was detected. However, the PCT effect was not as pronounced in treatments with uncontrolled birch stump sprouting, and in the treatments with densities of 2000 stems ha^{-1} there was no significant difference from the control. When the sprouts were removed annually the mean annual increment of dominant Norway spruce stems was, on average, 21 % higher compared to the same treatment with uncontrolled sprouting.

Both papers indicate the same result: that with a planting density of >2000 seedlings ha^{-1} the birch admixture will not survive the competition and the stands will develop into Norway spruce monocultures. However, in the PCT treatment with 1000 seedlings ha^{-1} of birch and Norway spruce, respectively (paper IV) and in the PCT simulations with low density planting treatments (paper III), the stands remained mixed.

The most severe obstacle to the vitality of the seedlings of tree species other than Norway spruce in the regeneration experiments was ungulate browsing five years after clearcut. The overall mean of damaged seedlings of the additional tree species was 77% and of these over 80 % were severely damaged. Only Norway spruce and birch had mean heights over 1 m and top heights of 3 and 4 meters. In current forestry, the spontaneous regeneration of broadleaved tree species is the only source of recruitment for these uncommercial tree species in forests. The high damage ratio due to ungulate browsing combined with the successful cultivation of Norway spruce will probably lead to mortality for most of the seedlings (papers II and III).

The simulations (paper III) were able to model visually the probable effect of browsing in the selections during PCT when comparing the traditional approach with selections of Norway spruce and birch (NSB) and the selection for multiple species at the stand level (mix). Figure 6 show the percentage of the tree species composition in every block and treatment (N=28), summarized for the experiments distributed over 20 ha, for two of the PCT alternatives. The spatial distribution of seedlings was considered in both, but only the NSB-alternative also have heights and planting investments in the selection criteria. The comparison of number of species in figure 6 is only to visualize the eventual effect that the selections in PCT could have at the landscape level.

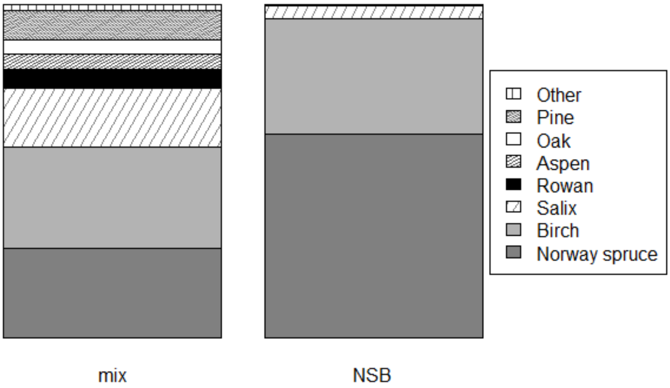

Figure 6. Visualization of the species % of stem number in two PCT simulations, aiming for multiple species (mix) and for production of Norway spruce and other species in gaps (NSB). Norway spruce includes both planted and naturally regenerated seedlings. The group “others” include all other species, not specified in legend , together amounting to < 2% of the total.

However, due to the browsing pressure and thereby suppressed heights of the seedlings for all the additional species, the mix-alternative is highly imaginary. The damaged seedlings, even if vital, will have difficulty keeping pace with the height increments of both birch and Norway spruce. Furthermore, if the browsing pressure remains, these seedlings will probably be repeatedly browsed during subsequent years. The findings from this regeneration experiments indicate that game management has a huge impact on future forests and the potential to establish mixed stands with more than one or two species. This finding is consistent with other studies in Fennoscandia (Herfindal *et al.*, 2015; Bergquist *et al.*, 2009; Edenius & Ericsson, 2007; Jalkanen, 2001; Kullberg & Bergstrom, 2001; Björse & Bradshaw, 1998) and the Forest Agency monitoring (Bergquist *et al.*, 2011) and in other managed forest ecosystems globally (Speed *et al.*, 2013; Elie *et al.*, 2009; Casabon & Pothier, 2007).

5 Conclusions

5.1 Practical implementation

Forest management is, first of all, influenced by a multitude of both incentives and limitations that sometimes are so hegemonic that they are mistaken for being deterministic. Soil scarification before planting of insecticide treated Norway spruce seedlings is legal and is the preferred method in current Swedish clearcut management. Not even the big storm Gudrun in 2005, which primary affected mature coniferous stands, made any difference to the choice of regeneration method (Valinger *et al.*, 2014). Clearcut management is determined by owner objectives, within which legislation and incentives from authoritie’s and stakeholders affect the limits of what is accepted or possible (Johansson, 2014; Johansson & Keskitalo, 2014; Kindstrand *et al.*, 2008).

Hopefully the results from this study and others, could promote management recommendations that are more diversified and tailored for a multitude of types of stand development (Gustafsson *et al.*, 2015; Agestam *et al.*, 2005). A similar approach, combining seed ecology and seedling survival with management (Dassot & Collet, 2015; Manso *et al.*, 2014; Eerikäinen *et al.*, 2007), resulted in the same conclusion as with the model framework presented in paper I: that with rather simplistic and general equations it is possible to build a complex model of the whole process. Hopefully these types of predictions about future stands will be useful to implement within forest modeling frameworks such as Heureka in Sweden and MOTTI in Finland (Salminen *et al.*, 2005), which are examples of complex forest simulation systems that are used both in research and in forest management.

With more precise predictions of birch seed supply, the soil disturbance rate could be chosen to meet the aims of the owner (Figure 7). When the supply is plentiful, it is possible to increase the birch seedling density and plant less Norway spruce if a mixture is desired. And the opposite; it could be difficult to establish a mixed forest based on natural regeneration in large clearcuts on mesic sites, especially in areas with low abundance of mature birch in the surroundings. When a Norway spruce monoculture is the main goal, no or very careful, soil scarification should be performed on such sites. However, the benefits of soil scarification for the planted seedlings are many and probably performed on these sites despite the increased competition from naturally regenerated species.

Precommercial thinning of young stands could be undertaken in various ways, there is a wide range of opinions regarding PCT intensity, timing of season and timing with respect to stand age, birch percentage and spatial distribution of saplings. Most importantly, the reduction in density, from more than 10 000 to 3000 stems ha^{-1} or less, is the major factor affecting the growth and yield of future crop trees. The largest saplings before PCT will remain dominant regardless of treatment and the size of a neighbor has a greater effect than the species. If the goal of establishment is a mixed stand throughout the rotation, the density has to be regulated during PCT to ensure the presence of unsuppressed birches. Density reduction has an effect on the seedlings already 1-1.5 m tall, but the competition from birch stump sprouting could be significant, at least in the first years after PCT.

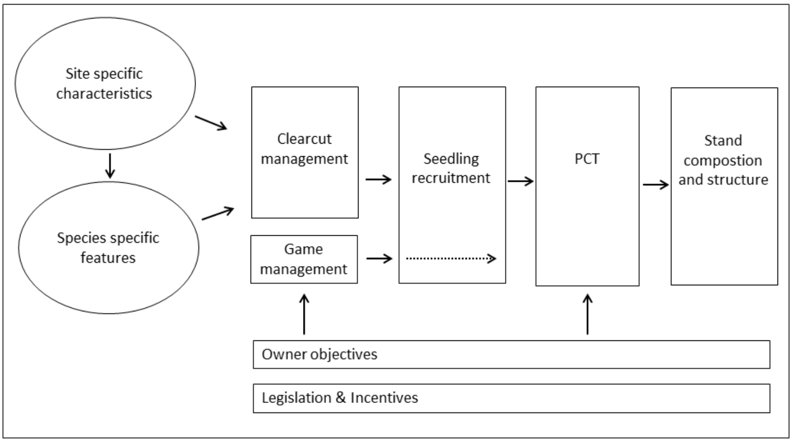

Figure 7. Flowchart covering the variables that affect and interact in the establishment of a new forest stand.

5.2 Future research

More precision should be possible when making the predictions of birch regeneration on a clearcut. The annual variation in seed production could be important, especially on sites with high fertility and fast ingrowth of competing vegetation on scarified surfaces. The masting behavior of birch is perhaps not of the same magnitude as for tree species with larger seed masses, but is still related to annual variations in climate. Future research into the annual variation of seed supply, for birch and for other broadleaves, could also be important from the perspective of climate change and for plant breeding.

Soil scarification is positive with respect to forest establishment, both for the survival and growth of planted conifers and for the facilitation of natural regeneration. However, the environmental consequences of large scale soil disturbance on field vegetation and soil microhabitats could be further investigated.

The stands developed during recent decades, with retention trees and broadleaved admixtures, will soon grow into closed canopy stands and further management of these forests may raise new questions regarding thinning regimes and operational guide lines. Management based on one dominant crop species may not suit the sustainability of multispecies forest. Recent research with efforts focused on producing guidelines for development and maintenance of mixed forests (Ducey & Knapp, 2010) in other ecosystems opens the way for similar discussions in a Swedish context. The management of mixed forest to deliver several objectives could possibly lead to new perspectives with respect to both planning and measuring forest growth.

When the heterogeneity of the tree population increases and old empirical data from controlled homogenous stands loses validity, then other variables could be considered instead, such as abiotic drivers of production, soil characteristics and climate variables. Improvements in large scale informatics, such as laser scanned elevation data, satellite-data based forest volume estimates and regional raster data for solar radiation, also suggest further developments in models of forest variables that combine empirical management, ecological theory and plant physiological relationships. In the future, a greater understanding of the growth and yield of mixed forests in Sweden will benefit from combining new data with process-based theories or hybrid models.

References

Abrahamsson, M., Jonsell, M., Niklasson, M. & Lindbladh, M. (2009). Saproxylic beetle assemblages in artificially created high-stumps of spruce (Picea abies) and birch (Betula pendula/pubescens) - does the surrounding landscape matter? *Insect Conservation and Diversity,* 2(4), pp. 284-294.

Agestam, E. (1985). *En produktionsmodell för blandbestånd av tall, gran och björk i Sverige : A growth simulator for mixed stands of pine, spruce and birch in Sweden.* Diss. Garpenberg: Swedish university of agricultural studies.

Agestam, E., Karlsson, M. & Nilsson, U. (2005). Mixed forests as a part of sustainable forestry in Southern Sweden. *Journal of Sustainable Forestry,* 21(2/3), pp. 101-117.

Aikens, M.L., Ellum, D., McKenna, J.J., Kelty, M.J. & Ashton, M.S. (2007). The effects of disturbance intensity on temporal and spatial patterns of herb colonization in a southern New England mixed-oak forest. *Forest Ecology and Management,* 252(1-3), pp. 144-158.

Ammer, S., Weber, K., Abs, C., Ammer, C. & Prietzel, J. (2006). Factors influencing the distribution and abundance of earthworm communities in pure and converted Scots pine stands. *Applied Soil Ecology,* 33(1), pp. 10-21.

Andersson, S.O. (1985). *Treatment of young mixed stands with birch and conifers*. (Broadleaves in boreal silviculture - an obstacle or an asset? Umeå, 1985 Rapporter - SLU, Institutionen för Skogsskötsel 14).

Andersson, S.O. & Björkdahl, G. (1984). Om björkstubbskottens höjdutveckling i ungdomsskedet. *Sveriges skogvårdsförbunds tidskrift,* 1984(3-4), pp. 61-67

Barbeito, I., Collet, C. & Ningre, F. (2014). Crown responses to neighbor density and species identity in a young mixed deciduous stand. *Trees-Structure and Function,* 28(6), pp. 1751-1765.

Bataineh, M.M., Wagner, R.G. & Weiskittel, A.R. (2013). Long-term response of spruce-fir stands to herbicide and precommercial thinning: observed and projected growth, yield, and financial returns in central Maine, USA.

Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 43(4), pp. 385-395.

Bergman, M., Iason, G.R. & Hester, A.J. (2005). Feeding patterns by roe deer and rabbits on pine, willow and birch in relation to spatial arrangement. *Oikos,* 109(3), pp. 513-520.

Bergquist, J., Eriksson, A. & Fries, C. (2011). *Skogsstyrelsen Polytax 5/7 återväxttaxering: Resultat från 1999-2009.* (Rapport Skogsstyrelsen, 2011).

Bergquist, J., Lof, M. & Orlander, G. (2009). Effects of roe deer browsing and site preparation on performance of planted broadleaved and conifer seedlings when using temporary fences. *Scandinavian Journal of Forest Research,* 24(4), pp. 308-317.

Bergqvist, G. (1999). Wood volume yield and stand structure in Norway spruce understorey depending on birch shelterwood density. *Forest Ecology and Management,* 122(3), pp. 221-229.

Bergqvist, G., Bergstrom, R. & Edenius, L. (2001). Patterns of stem damage by moose (Alces alces) in young Pinus sylvestris stands in Sweden. *Scandinavian Journal of Forest Research,* 16(4), pp. 363-370.

Bergqvist, G., Bergstrom, R. & Wallgren, M. (2014). Recent browsing damage by moose on Scots pine, birch and aspen in young commercial forests - effects of forage availability, moose population density and site productivity. *Silva Fennica,* 48(1).

Bergström, D., Bergsten, U., Hornlund, T. & Nordfjell, T. (2012). Continuous felling of small diameter trees in boom-corridors with a prototype felling head. *Scandinavian Journal of Forest Research,* 27(5), pp. 474-480.

Bergström, D., Bergsten, U. & Nordfjell, T. (2010). Comparison of Boom-Corridor Thinning and Thinning From Below Harvesting Methods in Young Dense Scots Pine Stands. *Silva Fennica,* 44(4), pp. 669-679.

Bielak, K., Dudzinska, M. & Pretzsch, H. (2014). Mixed stands of Scots pine (Pinus sylvestris L.) and Norway spruce Picea abies (L.) Karst can be more productive than monocultures. Evidence from over 100 years of observation of long-term experiments. *Forest Systems,* 23(3), pp. 573-589.

Björse, G. & Bradshaw, R. (1998). 2000 years of forest dynamics in southern Sweden: suggestions for forest management. *Forest Ecology and Management,* 104(1-3), pp. 15-26.

Bravo-Oviedo, A., Barreiro, S., Strelcova, K. & Pretzsch, H. (2014a). EuMIXFOR Introduction: integrating scientific knowledge in sustainable management of Mixed Forests. *Forest Systems,* 23(3), pp. 515-517.

Bravo-Oviedo, A., Pretzsch, H., Ammer, C., Andenmatten, E., Barbati, A., Barreiro, S., Brang, P., Bravo, F., Coll, L., Coronal, P., den Ouden, J., Ducey, M.J., Forrester, D.I., Giergiczny, M., Jacobsen, J.B., Lesinski, J., Loef, M., Mason, B., Metslaid, M., Matovic, B., Morneau, F., Motiejunaite, J., O'Reilly, C., Pach, M., Ponette, Q., del Rio, M., Short, I., Skovsgaard, J.P., Solino, M., Spathelf, P., Sterba, H., Stojanovic, D., Strelcova, K., Svoboda, M., Verheyenn, K., von Lupke, N. & Zlatanov, T.

(2014b). European Mixed Forests: definition and research perspectives. *Forest Systems,* 23(3), pp. 518-533.

Bremer, L. & Farley, K. (2010). Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodiversity and Conservation,* 19(14), pp. 3893-3915.

Brosofske, K.D., Froese, R.E., Falkowski, M.J. & Banskota, A. (2014). A Review of Methods for Mapping and Prediction of Inventory Attributes for Operational Forest Management. *Forest Science,* 60(4), pp. 733-756.

Brunet, J., De Frenne, P., Holmstrom, E. & Mayr, M.L. (2012). Life-history traits explain rapid colonization of young post-agricultural forests by understory herbs. *Forest Ecology and Management,* 278, pp. 55-62.

Bullock, J.M., Shea, K. & Skarpaas, O. (2006). Measuring plant dispersal: an introduction to field methods and experimental design. *Plant Ecology,* 186(2), pp. 217-234.

Canham, C.D. & Uriarte, M. (2006). Analysis of neighborhood dynamics of forest ecosystems using likelihood methods and modeling. *Ecological Applications,* 16(1), pp. 62-73.

Carnus, J.M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O'Hara, K. & Walters, B. (2006). Planted forests and biodiversity. *Journal of Forestry,* 104(2), pp. 65-77.

Casabon, C. & Pothier, D. (2007). Browsing of tree regeneration by white-tailed deer in large clearcuts on Anticosti Island, Quebec. *Forest Ecology and Management,* 253(1-3), pp. 112-119.

Chauvat, M., Titsch, D., Zaytsev, A.S. & Wolters, V. (2011). Changes in soil faunal assemblages during conversion from pure to mixed forest stands. *Forest Ecology and Management,* 262(3), pp. 317-324.

Clark, C.J., Poulsen, J.R., Levey, D.J. & Osenberg, C.W. (2007). Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *American Naturalist,* 170(1), pp. 128-142.

Collet, C., Ningre, F., Barbeito, I., Arnaud, A. & Piboule, A. (2014). Response of tree growth and species coexistence to density and species evenness in a young forest plantation with two competing species. *Annals of Botany,* 113(4), pp. 711-719.

Conner, L.G., Bunnell, M.C. & Gill, R.A. (2014). Forest diversity as a factor influencing Engelmann spruce resistance to beetle outbreaks. *Canadian Journal of Forest Research,* 44(11), pp. 1369-1375.

Dassot, M. & Collet, C. (2015). Manipulating seed availability, plant competition and litter accumulation by soil preparation and canopy opening to ensure regeneration success in temperate low-mountain forest stands. *European Journal of Forest Research,* 134(2), pp. 247-259.

Dirnberger, G.F. & Sterba, H. (2014). A comparison of different methods to estimate species proportions by area in mixed stands. *Forest Systems,* 23(3), pp. 534-546.

Ducey, M.J. & Knapp, R.A. (2010). A stand density index for complex mixed species forests in the northeastern United States. *Forest Ecology and Management,* 260(9), pp. 1613-1622.

Edenius, L. & Ericsson, G. (2007). Aspen demographics in relation to spatial context and ungulate browsing: Implications for conservation and forest management. *Biological Conservation,* 135(2), pp. 293-301.

Edenius, L., Ericsson, G. & Naslund, P. (2002). Selectivity by moose vs the spatial distribution of aspen: a natural experiment. *Ecography,* 25(3), pp. 289-294.

Eerikäinen, K., Miina, J. & Valkonen, S. (2007). Models for the regeneration establishment and the development of established seedlings in uneven-aged, Norway spruce dominated forest stands of southern Finland. *Forest Ecology and Management,* 242(2-3), pp. 444-461.

Elbakidze, M., Andersson, K., Angelstam, P., Armstrong, G.W., Axelsson, R., Doyon, F., Hermansson, M., Jacobsson, J. & Pautov, Y. (2013). Sustained Yield Forestry in Sweden and Russia: How Does it Correspond to Sustainable Forest Management Policy? *Ambio,* 42(2), pp. 160-173.

Elfving, B. *Growth modelling in the Heureka system. Swedish University of Agricultural Sciences, Faculty of Forestry.* *http://heurekaslu.org/wiki/Heureka_prognossystem_%28Elfving_rapportutkast%29.pdf* *[cited 12 feb 2015]*.

Elie, J.G., Ruel, J.C. & Lussier, J.M. (2009). Effect of Browsing, Seedbed, and Competition on the Development of Yellow Birch Seedlings in High-Graded Stands. *Northern Journal of Applied Forestry,* 26(3), pp. 99-105.

Fahlvik, N., Agestam, E., Ekö, P.M. & Linden, M. (2011). Development of single-storied mixtures of Norway spruce and birch in Southern Sweden. *Scandinavian Journal of Forest Research,* 26, pp. 36-45.

Fahlvik, N., Agestam, E., Nilsson, U. & Nystrom, K. (2005). Simulating the influence of initial stand structure on the development of young mixtures of Norway spruce and birch. *Forest Ecology and Management,* 213(1-3), pp. 297-311.

Fahlvik, N., Elfving, B. & Wikström, P. (2014). Evaluation of growth models used in the Swedish Forest Planning System Heureka. *Silva Fennica,* 48(2), pp. 1-17.

Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A. & Gustafsson, L. (2014). Can retention forestry help conserve biodiversity? A meta-analysis. *Journal of Applied Ecology,* 51(6), pp. 1669-1679.

Felton, A., Andersson, E., Ventorp, D. & Lindbladh, M. (2011). A comparison of avian diversity in spruce monocultures and spruce-birch polycultures in Southern Sweden. *Silva Fennica,* 45(5), pp. 1143-1150.

Felton, A., Lindbladh, M., Brunet, J. & Fritz, Ö. (2010). Replacing coniferous monocultures with mixed-species production stands: An assessment of the potential benefits for forest biodiversity in northern Europe. *Forest Ecology and Management,* 260(6), pp. 939-947.

Felton, A., Nilsson, U., Sonesson, J., A.M., F., Roberge, J.-M., Ranius, T., Ahlström, M., Bergh, J., Björkman, C., Boberg, J., Drössler, L., Fahlvik, N., Gong, P., Holmström, E., Keskitalo, E.C.H., Klapwijk, M.J., Laudon, H., Lundmark, T., Niklasson, M., Nordin, A., Pettersson, M., Stenlid, J., Sténs, A. & Wallertz, K. (2015). Replacing monocultures with mixed-species stands: Ecosystem service implications of two production forest mixture alternatives in Sweden. *Ambio,* 45(3), p. In press.

Fenner, M.T., K. (2005). *The ecology of seeds*: Cambridge University Press.

Finnish statistical yearbook of forestry (2014). Metsätilastollinen.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005). Global consequences of land use. *Science,* 309(5734), pp. 570-574.

Franceschini, T. & Schneider, R. (2014). Influence of shade tolerance and development stage on the allometry of ten temperate tree species. *Oecologia,* 176(3), pp. 739-749.

Fridley, J.D. (2001). The influence of species diversity on ecosystem productivity: how, where, and why? *Oikos,* 93(3), pp. 514-526.

Fries, C. (1984). Den frösådda björkens invandring på hygget [glasbjörk, vårtbjörk]. *Sveriges Skogsvårdsförbunds Tidskrift 1984,* 82((3-4)), p. 15.

Frivold, L.H. (1986). Natural regeneration of birch and Norway spruce on clearfelled areas in the East Norwegian lowlands in relation to vegetation type and moisture. *Meddelelser fra Norsk Institutt for Skogforskning,* 39, pp. 67-84.

Frivold, L.H. & Frank, J. (2002). Growth of mixed birch-coniferous stands in relation to pure coniferous stands at similar sites in south-eastern Norway. *Scandinavian Journal of Forest Research,* 17(2), pp. 139-149.

Fällman, K. (2005). *Aspects of precommercial thinning : private forest owners' attitudes and alternative practices.* Diss. Umeå: Swedish university of agricultural science.

Gamfeldt, L., Snall, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Froberg, M., Stendahl, J., Philipson, C.D., Mikusinski, G., Andersson, E., Westerlund, B., Andren, H., Moberg, F., Moen, J. & Bengtsson, J. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communication,* 4, p. 1340.

Gilichinsky, M., Heiskanen, J., Barth, A., Wallerman, J., Egberth, M. & Nilsson, M. (2012). Histogram matching for the calibration of kNN stem volume estimates. *International Journal of Remote Sensing,* 33(22), pp. 7117-7131.

Greene, D.F. & Johnson, E.A. (1989). A model of wind dispersal of winged or plumed seeds. *Ecology,* 70(2), pp. 339-347.

Greene, D.F. & Johnson, E.A. (1994). Estimating the mean annual seed production of trees. *Ecology,* 75(3), pp. 642-647.

Greene, D.F. & Johnson, E.A. (1995). Long-distance wind dispersal of tree seeds. *Canadian Journal of Botany-Revue Canadienne De Botanique,* 73(7), pp. 1036-1045.

Greene, D.F. & Johnson, E.A. (1996). Wind dispersal of seeds from a forest into a clearing. *Ecology,* 77(2), pp. 595-609.

Griess, V.C. & Knoke, T. (2011). Growth performance, windthrow, and insects: meta-analyses of parameters influencing performance of mixed-species stands in boreal and northern temperate biomes. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* 41(6), pp. 1141-1159.

Gundersen, V.S. & Frivold, L.H. (2008). Public preferences for forest structures: a review of quantitative surveys from Finland, Norway and Sweden. *Urban Forestry & Urban Greening,* 7(4), pp. 241-258.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B., Lohmus, A., Martinez Pastur, G., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A. & Franklin, J.F. (2012). Retention Forestry to Maintain Multifunctional Forests: A World Perspective. *Bioscience,* 62(7), pp. 633-645.

Gustafsson, L., Felton, A., Felton, A.M., Brunet, J., Caruso, A., Hjalten, J., Lindbladh, M., Ranius, T., Roberge, J.-M. & Weslien, J. (2015). Natural Versus National Boundaries: The Importance of Considering Biogeographical Patterns in Forest Conservation Policy. *Conservation Letters,* 8(1), pp. 50-57.

Götmark, F., Fridman, J., Kempe, G. & Norden, B. (2005). Broadleaved tree species in conifer-dominated forestry: Regeneration and limitation of saplings in southern Sweden. *Forest Ecology and Management,* 214(1-3), pp. 142-157.

Hamilton, N.R.S. (1994). Replacement and additive designs for plant competitions studies. *Journal of Applied Ecology,* 31(4), pp. 599-603.

Hansson, K., Olsson, B.A., Olsson, M., Johansson, U. & Kleja, D.B. (2011). Differences in soil properties in adjacent stands of Scots pine, Norway spruce and silver birch in SW Sweden. *Forest Ecology and Management,* 262(3), pp. 522-530.

Harper, J.L. (1977). *Population biology of plants*. London: Academic press.

Hazell, P. & Gustafsson, L. (1999). Retention of trees at final harvest - evaluation of a conservation technique using epiphytic bryophyte and lichen transplants. *Biological Conservation,* 90(2), pp. 133-142.

Hedwall, P.-O., Brunet, J., Nordin, A. & bergh, J. (2013). Changes in the abundance of keystone forest floor species in response to changes of forest structure. *Journal of Vegetation Science,* 24(2), pp. 296-306.

Herfindal, I., Tremblay, J.P., Hester, A.J., Lande, U.S. & Wam, H.K. (2015). Associational relationships at multiple spatial scales affect forest damage by moose. *Forest Ecology and Management,* 348, pp. 97-107.

Holm, S.O. (1994). Reproductive patterns of Betula-pendula and B-pubescens coll along a regional altitudinal gradient in northern Sweden. *Ecography,* 17(1), pp. 60-72.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs,* 75(1), pp. 3-35.

Hornberg, S. (2001). The relationship between moose (Alces alces) browsing utilisation and the occurrence of different forage species in Sweden. *Forest Ecology and Management,* 149(1-3), pp. 91-102.

Hynynen, J., Niemisto, P., Vihera-Aarnio, A., Brunner, A., Hein, S. & Velling, P. (2010). Silviculture of birch (Betula pendula Roth and Betula pubescens Ehrh.) in northern Europe. *Forestry,* 83(1), pp. 103-119.

Hynynen, J., Repola, J. & Mielikainen, K. (2011). The effects of species mixture on the growth and yield of mid-rotation mixed stands of Scots pine and silver birch. *Forest Ecology and Management,* 262(7), pp. 1174-1183.

Jacob, M., Leuschner, C. & Thomas, F.M. (2010). Productivity of temperate broad-leaved forest stands differing in tree species diversity. *Annals of Forest Science,* 67(5).

Jactel, H., Brockerhoff, E. & Duelli, P. (2005). A test of the biodiversity-stability theory: Meta-analysis of tree species diversity effects on insect pest infestations, and re-examination of responsible factors. In: SchererLorenzen, M., Korner, C. & Schulze, E.D. (eds) *Forest Diversity and Function: Temperate and Boreal Systems*. (Ecological Studies-Analysis and Synthesis, 176). Berlin: Springer-Verlag Berlin, pp. 235-262.

Jactel, H., Nicoll, B.C., Branco, M., Ramon Gonzalez-Olabarria, J., Grodzki, W., Langstrom, B., Moreira, F., Netherer, S., Orazio, C., Piou, D., Santos, H., Schelhaas, M.J., Tojic, K. & Vodde, F. (2009). The influences of forest stand management on biotic and abiotic risks of damage. *Annals of Forest Science,* 66(7).

Jalkanen, A. (2001). The probability of moose damage at the stand level in southern Finland. *Silva Fennica,* 35(2), pp. 159-168.

Johansson, J. (2012). Challenges to the Legitimacy of Private Forest Governance - the Development of Forest Certification in Sweden. *Environmental Policy and Governance,* 22(6), pp. 424-436.

Johansson, J. (2014). Why do forest companies change their CSR strategies? Responses to market demands and public regulation through dual-certification. *Journal of Environmental Planning and Management,* 57(3), pp. 349-368.

Johansson, J. & Keskitalo, E.C.H. (2014). Coordinating and implementing multiple systems for forest management: implications of the regulatory framework for sustainable forestry in Sweden. *Journal of Natural Resources Policy Research,* 6(2/3), pp. 117-133.

Johansson, K., Nilsson, U. & Örlander, G. (2013a). A comparison of long-term effects of scarification methods on the establishment of Norway spruce. *Forestry,* 86(1), pp. 91-98.

Johansson, K., Ring, E. & Hogbom, L. (2013b). Effects of pre-harvest fertilization and subsequent soil scarification on the growth of planted Pinus sylvestris seedlings and ground vegetation after clear-felling. *Silva Fennica,* 47(4), p. 18.

Johansson, T. (2003). Mixed stands in Nordic countries - a challenge for the future. *Biomass & Bioenergy,* 24(4-5), pp. 365-372.

Johansson, T. (2008). Sprouting ability and biomass production of downy and silver birch stumps of different diameters. *Biomass & Bioenergy,* 32(10), pp. 944-951.

Jonsson, B. (2001). Volume yield to mid-rotation in pure and mixed sown stands of Pinus sylvestris and Picea abies in Sweden. *Studia Forestalia Suecica*(211), pp. 19 pp.-19 pp.

Kalen, C. (2005). Deer browsing and impact on forest development. *Journal of Sustainable Forestry,* 21(2/3), pp. 53-64.

Karlsson, M. (2001). *Natural regeneration of broadleaved tree species in Southern Sweden - effects of silvicultural treatments and seed dispersal from surrounding stands.* Diss. Alnarp: Swedish University of Agricultural sciences.

Karlsson, M. & Nilsson, U. (2005). The effects of scarification and shelterwood treatments on naturally regenerated seedlings in southern Sweden. *Forest Ecology and Management,* 205(1-3), pp. 183-197.

Karlsson, M., Nilsson, U. & Orlander, G. (2002). Natural regeneration in clear-cuts: Effects of scarification, slash removal and clear-cut age. *Scandinavian Journal of Forest Research,* 17(2), pp. 131-138.

Kauppi, A., Kiviniitty, M. & Ferm, A. (1988). Growth habits and crown architecture of Betula pubescens ehrh of seed and sprout origin. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* 18(12), pp. 1603-1613.

Kauppi, A., Paukkonen, K. & Tela, H.L. (1991). The role of phenols in sprouting and wood decay of birches. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* 21(7), pp. 1066-1072.

Kelty, M.J. (1992). *Compare productivity of monocultures and mixed-species stands*. (Ecology and Silviculture of Mixed-Species Forests: A Festschrift for David M Smith, 40). Dordrecht: Kluwer Academic Publ.

Kelty, M.J. (2006). The role of species mixtures in plantation forestry. *Forest Ecology and Management,* 233(2-3), pp. 195-204.

Kelty, M.J., Camara-Cabrales, L. & Grogan, J. (2011). Red oak in southern New England and big-leaf mahogany in the Yucatan Peninsula: can mixed-species forests be sustainably managed for single-species production? *Journal of Sustainable Forestry,* 30(7), pp. 637-653.

Kelty, M.J. & Cameron, I.R. (1995). Plot designs for the analysis of species interactions in mixed stands. *Commonwealth Forestry Review,* 74(4), pp. 322-332, 386, 388.

Kerkhoff, A.J. & Enquist, B.J. (2007). The implications of scaling approaches for understanding resilience and reorganization in ecosystems. *Bioscience,* 57(6), pp. 489-499.

Kindstrand, C., Norman, J., Boman, M. & Mattsson, L. (2008). Attitudes towards various forest functions: A comparison between private forest owners and forest officers. *Scandinavian Journal of Forest Research,* 23(2), pp. 133-136.

Klang, F. & Eko, P.M. (1999). Tree properties and yield of Picea abies planted in shelterwoods. *Scandinavian Journal of Forest Research,* 14(3), pp. 262-269.

Knoke, T., Ammer, C., Stimm, B. & Mosandl, R. (2008). Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. *European Journal of Forest Research,* 127(2), pp. 89-101.

Korner, C. (2005). An introduction to the functional diversity of temperate forest trees. In: SchererLorenzen, M., Korner, C. & Schulze, E.D. (eds) *Forest Diversity and Function: Temperate and Boreal Systems*. (Ecological Studies-Analysis and Synthesis, 176), pp. 13-37.

Kruys, N., Fridman, J., Gotmark, F., Simonsson, P. & Gustafsson, L. (2013). Retaining trees for conservation at clearcutting has increased structural diversity in young Swedish production forests. *Forest Ecology and Management,* 304, pp. 312-321.

Kullberg, Y. & Bergstrom, R. (2001). Winter browsing by large herbivores on planted deciduous seedlings in southern Sweden. *Scandinavian Journal of Forest Research,* 16(4), pp. 371-378.

Laganière, J., Cavard, X., Brassard, B.W., Paré, D., Bergeron, Y. & Chen, H.Y.H. (2015). The influence of boreal tree species mixtures on ecosystem carbon storage and fluxes. *Forest Ecology and Management,* 354, pp. 119-129.

Langvall, O. & Ottosson Löfvenius, M. (2002). Effect of shelterwood density on nocturnal near-ground temperature, frost injury risk and budburst date of Norway spruce. *Forest Ecology and Management,* 168(1–3), pp. 149-161.

Lappi Seppälä, M. (1947). The rational silviculture of Birch woods in Finland. *Tidsskrift for Skogbruk,* 55(4/5), pp. 154-64.

Larson, B.C. (1992). *Pathways of development in mixed-species stands*. (Ecology and Silviculture of Mixed-Species Forests: A Festschrift for David M Smith, 40). Dordrecht: Kluwer Academic Publ.

Lehtosalo, M., Mäkelä, A. & Valkonen, S. (2010). Regeneration and tree growth dynamics of Picea abies, Betula pendula and Betula pubescens in regeneration areas treated with spot mounding in southern Finland. *Scandinavian Journal of Forest Research,* 25(3), pp. 213-223.

Li, J., Shi, J., Luo, Y.Q. & Heliövaara, K. (2012). Plant and insect diversity along an experimental gradient of larch-birch mixtures in Chinese boreal forests. *Turkish Journal of Agriculture and Forestry,* 36(2), pp. 247-255.

Li, J.L., Dang, Q.L. & Ambebe, T.F. (2009). Post-fire natural regeneration of young stands on clearcut and partial-cut and uncut sites of boreal mixedwoods. *Forest Ecology and Management,* 258(3), pp. 256-262.

Li, L., Weiner, J., Zhou, D., Huang, Y. & Sheng, L. (2013). Initial density affects biomass-density and allometric relationships in self-thinning populations of Fagopyrum esculentum. *Journal of Ecology,* 101(2), pp. 475-483.

Lindén, M. (2003). *Increment and yield in mixed stands with Norway spruce in southern Sweden.* Diss. Alnarp: Diss. (sammanfattning) Alnarp : Sveriges lantbruksuniv., 2003.

Lindén, M. & Agestam, E. (2003). Increment and yield in mixed and monoculture stands of Pinus sylvestris and Picea abies based on an experiment in southern Sweden. *Scandinavian Journal of Forest Research,* 18(2), pp. 155-162.

Lindenmayer, D.B., Franklin, J.F., Lohmus, A., Baker, S.C., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Martinez Pastur, G., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A. & Gustafsson, L. (2012). A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conservation Letters,* 5(6), pp. 421-431.

Lintunen, A. & Kaitaniemi, P. (2010). Responses of crown architecture in Betula pendula to competition are dependent on the species of neighbouring trees. *Trees-Structure and Function,* 24(3), pp. 411-424.

Lundqvist, L., Morling, T. & Valinger, E. (2014). Spruce and birch growth in pure and mixed stands in Sweden. *Forestry Chronicle,* 90(1), pp. 29-34.

Löf, M., Dey, D.C., Navarro, R.M. & Jacobs, D.F. (2012). Mechanical site preparation for forest restoration. *New Forests,* 43(5-6), pp. 825-848.

Man, R.Z. & Greenway, K.J. (2013). Effects of soil moisture and species composition on growth and productivity of trembling aspen and white spruce in planted mixtures: 5-year results. *New Forests,* 44(1), pp. 23-38.

Man, R.Z., Rice, J.A. & MacDonald, G.B. (2010). Five-year light, vegetation, and regeneration dynamics of boreal mixedwoods following silvicultural treatments to establish productive aspen-spruce mixtures in northeastern Ontario. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* 40(8), pp. 1529-1541.

Manso, R., Pukkala, T., Pardos, M., Miina, J. & Calama, R. (2014). Modelling Pinus pinea forest management to attain natural regeneration under present and future climatic scenarios. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* 44(3), pp. 250-262.

Mard, H. (1996). The influence of a birch shelter (Betula spp) on the growth of young stands of Picea abies. *Scandinavian Journal of Forest Research,* 11(4), pp. 343-350.

Mattila, U. (2005). Probability models for pine twisting rust (Melampsora pinitorqua) damage in Scots pine (Pinus sylvestris) stands in Finland. *Forest Pathology,* 35(1), pp. 9-21.

Mielikäinen, K. (1985). Effect of an admixture of birch on the structure and development of Norway spruce stands. In: *Communicationes Instituti Forestalis Fenniae,* pp. 79pp.-79pp.

Mielikäinen, K. (1994). Problems in modelling the development of mixed stands using data from temporary measurements. *Mixed stands: research plots, measurements and results, models. Proceedings from the Symposium of the IUFRO Working Groups S4.01, April 25-29, 1994 in Lousa/Coimbra, Portugal.,* pp. 271-279.

Milligan, H.T. & Koricheva, J. (2013). Effects of tree species richness and composition on moose winter browsing damage and foraging selectivity: an experimental study. *Journal of Animal Ecology,* 82(4), pp. 739-748.

Morin, X., Fahse, L., Scherer-Lorenzen, M. & Bugmann, H. (2011). Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters,* 14(12), pp. 1211-1219.

Nadrowski, K., Wirth, C. & Scherer-Lorenzen, M. (2010). Is forest diversity driving ecosystem function and service? *Current Opinion in Environmental Sustainability,* 2(1-2), pp. 75-79.

Nathan, R. & Muller-Landau, H.C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution,* 15(7), pp. 278-285.

Newmaster, S.G., Parker, W.C., Bell, F.W. & Paterson, J.M. (2007). Effects of forest floor disturbances by mechanical site preparation on floristic diversity in a central Ontario clearcut. *Forest Ecology and Management,* 246(2), pp. 196-207.

Nilsson, U. (1994). Development of growth and stand structure in Picea-abies stands planted at different initial densities. *Scandinavian Journal of Forest Research,* 9(2), pp. 135-142.

Nilsson, U., Gemmel, P., Johansson, U., Karlsson, M. & Welander, T. (2002). Natural regeneration of Norway spruce, Scots pine and birch under Norway spruce shelterwoods of varying densities on a mesic-dry site in southern Sweden. *Forest Ecology and Management,* 161(1-3), pp. 133-145.

Nordberg, M., Angelstam, P., Elbakidze, M. & Axelsson, R. (2013). From logging frontier towards sustainable forest management: experiences from boreal regions of North-West Russia and North Sweden. *Scandinavian Journal of Forest Research,* 28(8), pp. 797-810.

Oleskog, G., Grip, H., Bergsten, U. & Sahlen, K. (2000). Seedling emergence of Pinus sylvestris in characterized seedbed substrates under different moisture conditions. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* 30(11), pp. 1766-1777.

Olsthoorn, A.F.M.B., H.H.; Gardiner, J.J.; Pretzsch, H.; Hekhuis, H.J.; Franc, A. (1999). *Management of mixed-species forest: silviculture and economics*15): DLO Institute for Forestry and Nature Research (IBN-DLO), Wageningen, Netherlands.

Perala, D.A. & Alm, A.A. (1990a). Regeneration silviculture of birch - a review. *Forest Ecology and Management,* 32(1), pp. 39-77.

Perala, D.A. & Alm, A.A. (1990b). Reproductive ecology of birch - a review. *Forest Ecology and Management,* 32(1), pp. 1-38.

Petersson, M., Orlander, G. & Nordlander, G. (2005). Soil features affecting damage to conifer seedlings by the pine weevil Hylobius abietis. *Forestry,* 78(1), pp. 83-92.

Pettersson, N. (1993). The effect of density after precommercial thinning on volume and structure in Pinus sylvestris and Picea abies stands. *Scandinavian Journal of Forest Research,* 8(4), pp. 528-539.

Pilz, D. & Molina, R. (2002). Commercial harvests of edible mushrooms from the forests of the Pacific Northwest United States: issues, management, and monitoring for sustainability. *Forest Ecology and Management,* 155(1-3), pp. 3-16.

Porte, A. & Bartelink, H.H. (2002). Modelling mixed forest growth: a review of models for forest management. *Ecological Modelling,* 150(1-2), pp. 141-188.

Pretzsch, H. (2005). Diversity and productivity in forests: Evidence from long-term experimental plots. In: SchererLorenzen, M., Korner, C. & Schulze, E.D. (eds) *Forest Diversity and Function: Temperate and Boreal Systems*. (Ecological Studies-Analysis and Synthesis, 176), pp. 41-64.

Pretzsch, H. (2009). *Forest Dynamics, Growth and Yield: From Measurement to Model*. (Forest Dynamics, Growth and Yield: From Measurement to Model. Berlin: Springer-Verlag Berlin.

Prevost, M. & Dumais, D. (2014). Shelterwood cutting in a boreal mixedwood stand: 10-year effects of the establishment cut on growth and mortality of merchantable residual trees. *Forest Ecology and Management,* 330, pp. 94-104.

Radosevich, S.R., Hibbs, D.E. & Ghersa, C.M. (2006). Effects of species mixtures on growth and stand development of Douglas-fir and red alder. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* 36(3), pp. 768-782.

Reese, H., Nilsson, M., Pahlen, T.G., Hagner, O., Joyce, S., Tingelof, U., Egberth, M. & Olsson, H. (2003). Countrywide estimates of forest variables using satellite data and field data from the national forest inventory. *Ambio,* 32(8), pp. 542-548.

Reese, H., Nilsson, M., Sandstrom, P. & Olsson, H. (2002). Applications using estimates of forest parameters derived from satellite and forest inventory data. *Computers and Electronics in Agriculture,* 37(1-3), pp. 37-55.

Rejmanek, M. & Richardson, D.M. (1996). What attributes make some plant species more invasive? *Ecology,* 77(6), pp. 1655-1661.

Richards, A.E., Forrester, D.I., Bauhus, J. & Scherer-Lorenzen, M. (2010). The influence of mixed tree plantations on the nutrition of individual species: a review. *Tree Physiology,* 30(9), pp. 1192-1208.

Rothe, A. & Binkley, D. (2001). Nutritional interactions in mixed species forests: a synthesis. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* 31(11), pp. 1855-1870.

Salminen, H., Lehtonen, M. & Hynynen, J. (2005). Reusing legacy FORTRAN in the MOTTI growth and yield simulator. *Computers and Electronics in Agriculture,* 49(1), pp. 103-113.

Sarvas, R. (1948). A study of the regeneration of Birch in South Finland. *Metsatieteellisen tutkimuslaitoksen julkaisuja*(35, IV), pp. 91 pp.-91 pp.

Sarvas, R. (1952). On the flowering of Birch and the quality of seed crop. *Metsatieteellisen tutkimuslaitoksen julkaisuja,* 40(7), pp. 38-38.

Schippers, P. & Jongejans, E. (2005). Release thresholds strongly determine the range of seed dispersal by wind. *Ecological Modelling,* 185(1), pp. 93-103.

Schmidt, M., Veldkamp, E. & Corre, M.D. (2015). Tree species diversity effects on productivity, soil nutrient availability and nutrient response efficiency in a temperate deciduous forest. *Forest Ecology and Management,* 338, pp. 114-123.

Setiawan, N.N., Vanhellemont, M., Baeten, L., Dillen, M. & Verheyen, K. (2014). The effects of local neighbourhood diversity on pest and disease damage of trees in a young experimental forest. *Forest Ecology and Management,* 334, pp. 1-9.

Shinozaki, K. & Kira, T. (1956). Intraspecific competition among higher plants VII. Logistic theory of the C-D effect. *Jour Inst Polytech Osaka City Univ Ser D Biol,* 7, pp. 35-72.

Skogsdata (2014). Tema: Biologisk mångfald). Umeå: Umeå : Institutionen för skoglig resurshushållning, Sveriges lantbruksuniversitet.

Speed, J.D.M., Austrheim, G., Hester, A.J., Solberg, E.J. & Tremblay, J.P. (2013). Regional-scale alteration of clear-cut forest regeneration caused by moose browsing. *Forest Ecology and Management*, 289, pp. 289-299.

Stoyan, D. & Wagner, S. (2001). Estimating the fruit dispersion of anemochorous forest trees. *Ecological Modelling,* 145(1), pp. 35-47.

Swedish FSC Standard for Forest Certification including SLIMF indicators. (2010). FSC.

Swedish statistical yearbook of forestry (2014).

Söderberg, U. (1986). *Funktioner för skogliga produktionsprognoser : tillväxt och formhöjd för enskilda träd av inhemska trädslag i Sverige = Functions for forecasting of timber yields : increment and form height for individual trees of native species in Sweden.* Diss. Uppsala: SLU.

Tham, A. (1994). Crop plans and yield predictions for Norway spruce (Picea abies (L.) Karst.) and birch (Betula pendula Roth and Betula pubescens Ehrh.) mixtures. *Studia Forestalia Suecica,* 0(195), pp. 1-21.

Tomppo, E., Olsson, H., Stahl, G., Nilsson, M., Hagner, O. & Katila, M. (2008). Combining national forest inventory field plots and remote sensing data for forest databases. *Remote Sensing of Environment,* 112(5), pp. 1982-1999.

Ulvcrona, K.A., Karlsson, L., Backlund, I. & Bergsten, U. (2013). Comparison of silvicultural regimes of lodgepole pine (Pinus contorta) in Sweden 5 years after precommercial thinning. *Silva Fennica,* 47(3).

Waelder, K., Naether, W. & Wagner, S. (2009). Improving inverse model fitting in trees-Anisotropy, multiplicative effects, and Bayes estimation. *Ecological Modelling,* 220(8), pp. 1044-1053.

Wagner, R.G. (2008). Long-term spatial and structural dynamics in Acadian mixedwood stands managed under various silvicultural systems. *Canadian Journal of Forest Research,* 38(3), pp. 498-517.

Walfridsson, E. (1976). *[Competition from broadleaved trees in young conifer plantations]*. Diss.: Master th. Swedish university of Agricultural Science.

Valinger, E. & Fridman, J. (2011). Factors affecting the probability of windthrow at stand level as a result of Gudrun winter storm in southern Sweden. *Forest Ecology and Management,* 262(3), pp. 398-403.

Valinger, E., Kempe, G. & Fridman, J. (2014). Forest management and forest state in southern Sweden before and after the impact of storm Gudrun in the winter of 2005. *Scandinavian Journal of Forest Research,* 29(5), pp. 466-472.

Valkonen, S. & Valsta, L. (2001). Productivity and economics of mixed two-storied spruce and birch stands in Southern Finland simulated with empirical models. *Forest Ecology and Management,* 140(2-3), pp. 133-149.

Wallertz, K. & Petersson, M. (2011). Pine weevil damage to Norway spruce seedlings: effects of nutrient-loading, soil inversion and physical protection during seedling establishment. *Agricultural and Forest Entomology,* 13(4), pp. 413-421.

van Beest, F.M., Mysterud, A., Loe, L.E. & Milner, J.M. (2010). Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. *Journal of Animal Ecology,* 79(4), pp. 910-922.

Vehviläinen, H. & Koricheva, J. (2006). Moose and vole browsing patterns in experimentally assembled pure and mixed forest stands. *Ecography,* 29(4), pp. 497-506.

Weiskittel, A.R., Kenefic, L.S., Li, R., Brissette, J., Weiskittel, A.R., Kenefic, L.S., Li, R. & Brissette, J. (2011). Stand structure and composition 32 years after precommercial thinning treatments in a mixed northern conifer stand in central Maine. *Northern Journal of Applied Forestry,* 28(2), pp. 92-96.

Wikström, P., Edenius, L., Elfving, B., Eriksson, L.O., Lamas, T., Sonesson, J., Ohman, K., Wallerman, J., Waller, C. & Klinteback, F. (2011). The Heureka forestry decision support system: an overview. *Mathematical and Computational Forestry and Natural Resources Sciences,* 3(2), pp. 87-94.

Vila, M., Vayreda, J., Comas, L., Josep Ibanez, J., Mata, T. & Obon, B. (2007). Species richness and wood production: a positive association in Mediterranean forests. *Ecology Letters,* 10(3), pp. 241-250.

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