Regeneration in Continuous Cover Forestry Systems

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Abstract

The overall aim of the studies underlying this thesis has been to qualify and quantify the regeneration of tree species in a range of typical growing environments of possible Continuous Cover Forestry (CCF) silvicultural systems in boreal forests of northern Sweden. Data presented in Papers I and II show that the light environment did not differ significantly between points at different distances to trees, but it was clearly affected by the stand stem density (SSD). On a north-facing slope, the emergence rates of direct-seeded seedlings were highest (50 and 44% of germinable *Pinus sylvestris* and *Pices abies* seeds, respectively) in a stand with an SSD of 150. In contrast, on a slope with a southern aspect the conditions in SSD 0 favoured emergence of *P. sylvestris* (41%). For planted *P. abies,* fertilised seedlings in SSD 0 grew the most (22.2 cm in height on the North and 34.2 cm on the South slope). Establishment of both *P. sylvestris* and *P.abies* seedlings was more controlled by the general (light) conditions of the stand than their orientation and distance with respect to the nearest tree.

In Paper III, seedling survival and growth were compared between a clear-cut, a multi-layered shelterwood (MLS), and a single-layered shelterwood (SLS). The needle and root biomass of seedlings of both species, growing in identical (good) soil conditions, was highest in the clear-cut (*P. sylvestris* 63 and 14 g, respectively; *P. abies* 34 and 12 g, respectively). With those soil conditions, there were also no significant differences in growth, at least for *P. sylvestris,* between the MLS and SLS, although with increased belowground competition seedlings grew more slowly in the MLS.

In Papers IV and V, the establishment and growth of *Betula pendula*, *Populus tremula*, *P. sylvestris*, *Larix sibirica*, *Abies lasiocarpa*, and *P. abies*, planted in a Chequered-Gap-Shelterwood-System (CGSS) with 0.135 ha gaps under a shelter of pine forest, were compared in a 30-year-old ("younger") stand and a 50-year-old ("older") stand. Solar radiation transmission in the CGSS was simulated by modelling, and the results of the model were further related to seedling height growth by seedling positions within gaps. In the older stand, it was more favourable for seedlings to grow in south-facing parts of a gap with higher transmission. An approach for estimating biomass based on image inventories was applied, which showed that seedlings generally developed more biomass during the study period in gaps than at edges and in the forest (586.4±93.5 versus 203.8±22.3 and 121.3±24.1 cm^2 silhouette areas, respectively, in the older stand for example). To conclude, the results from this thesis have shown that tree regeneration and early growth can be maximized in a CCF system by matching growth environments and species, based especially on the considered species' light tolerance.

Keywords: *A. lasiocarpa, B. pendula,* Biomass, Continuous Cover Forestry, Direct seeding, Fertilisation, Forest gap, *L. sibirica,* Light, Shelterwood, Solar radiation simulation model, *Picea abies, Pinus sylvestris, P. tremula*

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Svensk sammanfattning

Det övergripandet syftet med de fem studier som denna avhandling baseras på, har varit att ta fram mer kunskap om hur olika faktorer påverkar vid skogsföryngring i kontinuitetsskogsbruk i boreal skog i norra Sverige. Studie I och II, i grandominerade bestånd, visade att ljusmiljön inte skiljde sig signifikant mellan olika avstånd till skärmträd, men var klart påverkad av beståndets stamtäthet (hygge med 0, skärmställning med 150 eller orörd skog med 500 stammar per hektar). På en nordlig sluttning var plantbildningen störst, 50 och 44% av grobara frön av *Pinus sylvestris* (tall) respektive *Pices abies* (gran), i skärmställningen medan förhållandena på hygge var de mest gynnsamma för plantbildning av tall (41%) på en sydlig sluttning. Av planterade granar växte gödslade plantor på hygge mest (22.2 cm i höjd på den nordliga sluttningen respektive 34.2 cm på den sydliga), medan gödsling inte kunde påskynda tillväxt av plantor med sämre ljustillgång. Beståndstyp hade större betydelse för etablering av både tall- och gran plantor, i enlighet med ljusmiljön, än plantornas individuella placering i förhållande till närmaste skärmträd.

I Studie III jämfördes plantöverlevnad och -tillväxt mellan ett hygge, en skiktad och en hög skärmställning. Båda arternas barr- och rotbiomassa var högst på hygget när de växte i likvärdig jord med god näringsstatus (63 respektive 14 g för tall och 34 respektive 12 g för gran). Med de markförhållandena var det inte heller någon signifikant skillnad i tillväxt, åtminstone för tall, mellan de olika skärmställningarna, medan ökad rotkonkurrens innebar att plantorna växte långsammare i den flerskiktade skärmställningen.

I Studie IV och V jämfördes etablering och tillväxt av *Betula pendula*, *Populus tremula*, *P. sylvestris*, *Larix sibirica*, *Abies lasiocarpa* och *P. abies*, som planterats i 0.135 ha stora luckor bildande ett schackrutigt huggningsmönster (så kallat ”Chequered-Gap-Shelterwood-System”; CGSS) i ett 30-årigt (”yngre”) samt 50-årigt (”äldre”) tallbestånd. Transmissionen av solstrålning i CGS-systemet simulerades med hjälp av en modell, och resultaten från modellen relaterades sedan till position och höjdtillväxt hos planterade plantor i luckorna. I det äldre beståndet var det mer gynnsamt för plantorna att växa i luckornas nordliga delar (de som vetter mot söder) med högre transmission. En metod att skatta biomassa baserad på bildanalys användes, vilket visade att plantorna under perioden för studien generellt utvecklade mer biomassa i luckorna än vid beståndskanterna eller i skogen (586.4±93.5 mot 203.8±22.3 respektive 121.3±24.1 cm^2 silhuettarea, med det äldre beståndet som exempel). Avhandlingens resultat visar sammanfattningsvis att föryngring och tidig tillväxt av trädarter i skötselsystem inom kontinuitetsskogsbruk kan optimeras med rätt kombination av miljö och art, med artens ljustolerans som främsta urvalskriterium.

Sökord: *A. lasiocarpa, B. pendula,* Biomassa, Gödsling, Kontinuitetsskogsbruk, *L. sibirica,* Ljus, Luckhuggning, *Picea abies, Pinus sylvestris, P. tremula,* Simuleringsmodell för solstrålning, Skärmställning, Sådd

Till mina pojkar

Contents

List of Publications

This thesis summarises and discusses the following five papers, which will be referred to by their respective roman numerals.

I. Erefur, C., Bergsten, U. & de Chantal, M. (2008). Establishment of direct seeded seedlings of Norway spruce and Scots pine: effects of stand conditions, orientation and distance with respect to shelter tree, and fertilisation. *Forest Ecology and Management* 255(3-4): 1186-1195.

II. Erefur, C., Bergsten, U., Lundmark, T. & de Chantal, M. Establishment of planted Norway spruce and Scots pine seedlings: effects of stand conditions, orientation and distance with respect to shelter tree and fertilisation. *Submitted.*

III. Erefur, C., Bergsten, U., Ottosson Löfvenius, M. & Lundmark, T. Early growth of Scots pine and Norway spruce seedlings planted in shelterwoods with varying light regimes but the same soils. *Manuscript.*

IV. Erefur, C., Bergsten, U., Ottosson Löfvenius, M., Lundmark, T. & de Chantal, M. Solar radiation regime and the growth of Scots pine and Norway spruce planted in the gaps of a Chequered-Gap-Shelterwood-System. *Submitted.*

V. Erefur, C., Bergsten, U., Lundmark, T., Ottosson Löfvenius, M., & de Chantal, M. Establishment and growth of tree seedlings with differing light tolerance in a gradient between gap and forest in a Chequered-Gap-Shelterwood-System. *Manuscript.*

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Introduction

Needs of society – demands on forestry

All silvicultural systems began as a set of practices developed in response to local, site-specific needs and ecological conditions. Silviculture is practiced with the aim of utilizing the primary product (e.g., timber and pulpwood) for a certain purpose, and silvicultural progress has directly followed socio-economic trends (Puettmann *et al.*, 2009). In Sweden forestry has been of great importance for the economy of the country for a long time. During periods of fairly constant social and environmental conditions, such as during the 1950s through the 1970s, there was little change in the objectives for cultivating forests (ibid.). However, since World War II there has been a gradual mechanization of applied methods, and the modern forest worker is more than ten times more productive than counterparts in the 1950's since nearly every link in the timber production chain is now mechanized. The chainsaw has been fully replaced by the harvester, a one-man, technically sophisticated, off-road machine used for felling, delimbing, and crosscutting in one continuous operation (Axelsson, 1998). In addition, during the 20th century silviculture became increasingly active, developing from selective logging of large (generally *Pinus sylvestris*) trees to harvesting by clear-cutting, which has had far-reaching consequences for boreal forest landscapes (Östlund *et al.*, 1997).

Silviculture is now undergoing a further massive change since forestry must meet a wide array of sometimes-conflicting demands (as illustrated in Figure 1), using a combination of traditional approaches, current scientific understanding and legal stipulations to choose between options that profoundly affect the management, structure and composition of forests (Puettmann *et al.*, 2009). The challenge for sustainable forest management is to define the attributes of forested ecosystems that are ecologically, socio-economically and culturally important, and maximize these ecosystem services or goods in the face of change. Addressing these issues requires attention to, and management of, interactive controls, which requires (*inter alia*) sound understanding of disturbance regimes, plant functional types, and soil resources (Chapin III *et al.*, 2002). According to the global Convention on Biological Diversity (CBD;

Anon., 1993b), the biological diversity of ecosystems should be maintained, be capable of sustainable exploitation, and there should be a fair distribution of the resources linked to this diversity. Meeting these demands calls for multifunctional and flexible forestry practices (Gadow *et al.*, 2007).

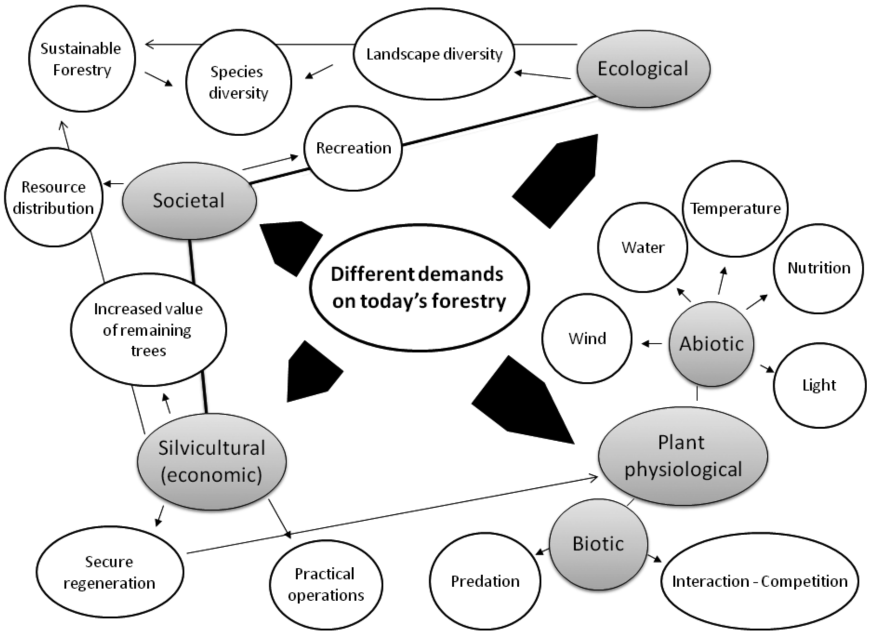

Figure 1. Schematic diagram of the multiple demands on modern forestry: societal, silvicultural, ecological, and plant physiological.

Needs of a tree

The development and application of regeneration practices, for which a need arose as silviculture intensified, has in turn been directly linked to specific ecological, as well as social and economic conditions. Important components of plant responses to closure in forests and gap creation include physiological and allocation responses to fluctuating light environments over time scales of years or decades (Ackerly & Bazzaz, 1995). Many environmental factors influence these responses. The most important include the length of time during which conditions are suitable for photosynthesis and soil resources. However, environmental stresses reduce the efficiency with which plants can use light to gain carbon, while aspects such as myccorhizal activity (Jentschke *et al.*, 2001), competition within their neighbourhood (Malcom & Ibrahim, 1993), soil temperature, associated nitrogen mineralization rates (Domisch *et al.*, 2002), fertilisation and irrigation treatments (Ingerslev & Hallbäcken, 1999; Albough *et al.*, 1998) are all of major importance for allocation patterns. There are also wide species- and genotype-dependent ranges in responses to all of these factors. Further, the physiological activities within each plant must be balanced between shoots and roots to optimise its growth, within its genetic and ecological constraints. Hence, plants adjust acquisition via adaptive mechanisms that maximize their capture of, and minimize limitation by, the most limiting resource (Chapin III *et al.*, 2002), within these constraints.

Alteration of stand structure influences the ecosystem

The structure of a forest has a direct bearing on the energy, hydrology and nutrient cycles within the forest ecosystem. An alteration of stand structure will influence the functioning of the ecosystem and have direct effects on site microclimate, water balance and soil fertility, thereby inducing physiological responses in seedlings (Grossnickle, 2000). A shift in energy balance occurs when there is removal of the forest canopy (Oke, 1987), since a much higher amount of radiant energy will then reach the soil surface. Such changes in energy distribution clearly alter the temperature of the soil and air, as well as evaporation from the ground and transpiration from leaves near the ground (Grossnickle, 2000). A mature forest stand has quite high transpiration rates, which reduce and regulate stream flow through the ecosystem. The hydrological cycle is dramatically altered in a clear-cut, which is characterized by low stand transpiration leading to increased stream flow, and potentially high amounts of available soil water (ibid.). The amount of soil water available for seedling emergence and establishment also depends on the texture and structure of the soil. In climax forests nutrient cycling is slow since most nutrients are bound in the tree biomass or organic matter on the ground. The removal of biomass through harvesting reduces the nutrient content of the site and the remainder, which is mostly left on the forest floor, is rapidly cycled through decomposition and mineralization (ibid.).

Solar radiation

Like all plants, tree seedlings are influenced by many factors during germination, establishment and later stages of growth and development (de Chantal *et al.*, 2003a, b, 2004; Winsa & Sahlén, 2001; Oleskog *et al.*, 2000; Oleskog & Sahlén, 2000b; Oleskog & Sahlén, 2000a; Goulet, 1995; Winsa, 1995b). Specific conditions will vary, depending on the site and stand environment, i.e., the light, water and nutrient conditions, and the plant material. Natural conditions provide environmental heterogeneity in both space and time since there are variations at all levels from micro to macro (e.g. seconds to decades).

The effect of variation at these different scales depends on the plant's rate of response to physiological and ecological processes of interest. Each seedling experiences fluctuations and individual acclimation may be an important component of responses and performance through time. For example (in the northern hemisphere), in forest gaps individuals located on the west side receive more light in the morning hours when CO_2 levels are high and tissue water potential is less negative. The plants can then photosynthesize at a high rate. In contrast, plants located on the east side of the gap receive sunlight mainly in the afternoon, when CO_2 levels are no longer high and plant tissue water potential has become more negative. Hence, resource processing can be greatly reduced, depending on the ability of the plant to hold and protect resources until other essential resources become available (Bazzaz & Grace, 1997). In addition, transient sun patches in the understorey of a forest provide bursts of high energy that are critical for carbon gain in these environments. The utilization of this energy depends on the duration of the sun patch because various physiological processes, like photosynthesis, stomatal opening and enzyme activity, respond at different rates to a change in the radiation environment (Ackerly & Bazzaz, 1995).

Whole plant carbon gain depends on the temporal scale of diurnal fluctuations in light environments, even when the total amount of light is constant (Wayne & Bazzaz, 1993). Leaf area (LA) is the major factor governing the amount of light intercepted by individual leaves in the canopy, but there are only modest variations in photosynthetic capacity per unit LA because leaves with a high photosynthetic capacity per unit leaf biomass also have a high specific leaf area (SLA; ratio of leaf area to leaf mass). However, diverse mechanisms of adjusting to variations in light have evolved. Notably, leaves adjust their stomatal conductance and photosynthetic capacity via responses that optimize carbon gain in different light environments. In addition, some photosynthetic responses of plants are almost instantaneous, but through physiological acclimation plants produce different types of leaves such as sun and shade leaves that are morphologically and biochemically adapted to different conditions. Sun leaves have more cell layers and a higher photosynthetic capacity than shade leaves, while the latter have higher contents of light harvesting pigments. There are also genetic adaptations to variations in light, but mediated via the same mechanisms as for acclimation. Plants may also maximize their leaf area by producing more leaves, thin leaves (shade) or cylindrical leaves (sun), or adjusting their leaf angle according to the sun's position (Chapin III *et al.*, 2002).

An important factor influencing the choice of silvicultural system is the light requirements of the species to be regenerated: shade-tolerant species can be expected to grow in small gaps of 0.05 ha or even less (Mason *et al.*, 1999); intermediate species can grow under canopies, but for good seedling growth quite early canopy removal is required; and light-demanding species will require very light canopies or open areas to grow satisfactorily. All species can occur as advance regeneration underneath an overstorey, but if a seedling is not sufficiently shade-tolerant it will not be able to survive and grow for any length of time. Species also differ in their rates of responses to environmental changes, and the phenotypic plasticity of an individual has a strong influence on how the scale of environmental fluctuations influences its overall performance, i.e., growth, survival and reproductive output (Ackerly & Bazzaz, 1995).

Water availability and growth

Water limitation reduces the capacity of individual leaves to match CO_2 supply with light availability, and extreme temperatures will also limit carbon uptake. The growth reduction at low soil water potential (dry conditions) is most likely due to the inhibition of sensitive processes such as cell elongation and protein synthesis. Above-ground plant parts respond more strongly than roots to reductions in soil water potential. Since photosynthesis is less affected than leaf growth, photosynthate export from leaves as well as root growth may be enhanced, with the effect that the evaporative surface is reduced relative to the water-absorbing surface (Chapin III *et al.*, 2002).

Nutrient uptake and use

Most plants need more nitrogen than other essential elements except carbon, oxygen, and hydrogen. Only a small fraction of the nitrogen store in the soil is available to plant roots at any given moment. As far as nitrogen is concerned, the end products of the decomposition process are ammonium ions. Inorganic nitrogen is usually fully reduced, ammonium, or fully oxidized, nitrate. Nitrate ions are easily taken up by roots, but at a higher energy cost than ammonium ions (Tamm 1991).

Many factors influence nutrient uptake by vegetation, but three of the most important are nutrient supply rate from the soil, root length, and root activity. Nutrient supply by the soil rather than plant traits determine between-biome differences in nutrient uptake by vegetation, but root length is the major factor governing which plants in an ecosystem will compete most successfully for limited supplies of nutrients (Chapin III *et al.,* 2002). Root biomass differs less than aboveground biomass among ecosystems at steady state, due to counteracting effects of production and allocation (ibid.). A way in which many plants increase their capacity to acquire nutrients is through symbiotic associations with mycorrhizal fungi, which increase the volume of soil they can exploit. Under conditions of nutrient limitation plants further maximize root length and the root growth is concentrated in spots of relatively high nutrient availability. Plants also alter the kinetics of nutrient uptake in response to changes in their requirements for nutrients and they are capable of maximizing their capacity to absorb elements that most strongly limit growth (ibid.). Active transport is the major mechanism whereby plants absorb potentially limiting nutrients from the soil solution at the root surface. Nutrient use efficiency is also greatest when production is nutrient-limited, thus nutrient supply affects growth more than it affects nutrient concentrations within plant tissues. Plants can maximize their nutrient use efficiency in infertile soils by reducing nutrient losses more than by increasing nutrient productivity. Consequently, in highly productive ecosystems producing large amounts of aboveground biomass there is relatively low production of root biomass, since the plants have relatively little need to allocate resources to roots in order to increase nutrient uptake from the soil (ibid.). According to Ingestad and Ågren (1995) two kinds of growth-determining factors can be distinguished: 1) mass transport and 2) factors that influence mass transport rates, such as light and water availability, genome, nutrient status and temperature. Avenues whereby nutrients are lost from plants include senescence, various kinds of disturbances, and diseases.

In addition to abiotic factors, biotic factors like herbivory and predation on tree seeds and seedlings may have major effects on establishment. According to a comparison of uncut forest, shelterwood, and clear-cuts by Nystrand and Granström (2000), predation on *P. sylvestris* seedling is negatively related to stand disturbance. Seed predation on the other hand, decreased in the order shelterwood>uncut forest>clear-cut. However, there were generally large between-site variations in predation. The most important seed predators were carabids, while juvenile seedlings were predated mainly by slugs (ibid.).

Continuous Cover Forestry

The establishment, growth and development of trees are all strongly affected by interactions with and between numerous physico-chemical environmental variables. For different plant materials and phases of seed/seedling development, changes in stand type and site conditions together with the location of seedlings relative to the surrounding trees create complex mosaics of light and water regimes, nutritional status, and risks of mechanical disturbances (such as rain/snow, litter fall, and predation; Hagner, 1962). Continuous Cover Forestry (CCF) provides a possible way to meet the needs of society and at the same time create conditions for successful regeneration and growth of specific tree species, using so-called "shelterwoods".

The shelterwood system first became popular in central Europe as it provided a good compromise between economic and ecological constraints and also permitted variations in cutting intensity to reflect the density and growth of regeneration. During its early development, users of the shelterwood method focused on providing optimal conditions for regeneration (Puettmann *et al.*, 2009). Over time silviculturists have noticed, through careful observation, that the tree overstory provides frost protection and suppresses development of competing vegetation, thus allowing new tree germinants to become established. The shelter trees were specifically selected to provide seed sources and protection for the regeneration. The diurnal amplitude of ground temperature is less pronounced in a shelterwood than on a clear-cut since the overstorey trees reduce incoming solar radiation as well as the nocturnal outgoing long-wave radiation, thus reducing the net radiation at the forest floor. Hence there are fewer summer frosts and less frost heaving (Örlander & Karlsson, 2000; Örlander & Langvall, 1997; Hannerz & Gemmel, 1994). Other beneficial effects of shelter trees for seedlings, besides reductions in competing vegetation, include less wind exposure, more stable soil water contents (on a clear-cut there can easily be an excess of water when the mature stand is removed, but also droughts as a result of more extreme temperatures; Holgen & Hånell, 2000). However, it became apparent that seeds can germinate under fairly limited light conditions, but that seedlings require more light for continuous growth and survival.

Many kinds of shelterwood, including both group and single-tree selection systems, have been adopted at various times. For example: in Germany, "Femelschlag" (a group selection system) has been very successful in some localities, and in Canada a larger-scale system with 40-150 hectares cut blocks has been applied in recent decades (Potvin *et al.*, 1999; DeLong & Tanner, 1996). Indeed, as early as the middle of the 19th century a debate about the relative merits of regular and irregular silviculture started in Europe. This has led to the present CCF system, which involves the maintenance of a forest canopy during the regeneration phase. Clear-felling of areas much more than two tree heights wide without the retention of some mature trees is generally avoided (Mason *et al.*, 1999). The rationale of contemporary CCF is to provide more diverse forests for multi-purpose benefits, and the adoption of CCFS on any scale will require changes in both silvicultural practices and management thinking. However, this does not mean abandoning stand management or timber production. CCF is more than a silvicultural system, it is an approach to forest management (ibid.). Some of the advantages of CCF are that it has less adverse visual impact than clear-felling, and increases within-stand structural and species diversity. Gardiner et al. (2005) have also demonstrated that complex CCF structures can reduce wind loading on the dominant trees, in experiments with model trees in a wind tunnel, supporting the theory that complex CCF structures can be more stable than even-aged stands. They showed that in the presence of smaller sub-canopy trees a complex structure reduced the wind loading on the largest trees in the stand compared with a simple structure or a stand in transformation. This was due to sheltering effects within the canopy since small differences in mean wind speed and turbulence above the canopy were found between the different stand structures tested. With CCF there are fewer disturbances of the forest ecosystem and greater abundance of sheltered microsites for regenerating seedlings, which may be advantageous in the context of extreme weather conditions following climate change. There are also usually lower regeneration costs and higher production of large diameter and high quality logs (Mason *et al.,* 1999). In suitable stands, CCF can complement conventional forestry methods in the Nordic counties by favouring ecological, cultural and social factors. This is especially attractive in Sweden since ecological and socio-cultural factors have as much or almost as much importance as economic considerations in Swedish forest policies (cf. Anon., 1993a). In Sweden, CCF is defined (according to Swedish Forest Agency; Cedergren, 2008) as forest management performed without clear-cutting, thus it encompasses measures, methods as well as systems for managing the forest.

Prediction of the effects of silvicultural manipulations must be based on the spatial as well as temporal dynamics of forest responses to different kinds, sizes, frequencies and intensities of disturbances (Coates & Burton, 1997). Successful strategies must be based on an understanding of interactions among shelter, vegetation, the physical environment, and the responses of regenerating tree species.

Objectives

In the context of a societal need to design and apply silvicultural systems that provide both secure regeneration and more complex, diverse stand structures, the overall aim of the studies underlying this thesis has been to explore practically applicable forestry methods that can be used in CCF systems. The work has focused on (i) qualifying and quantifying the regeneration of tree species in a range of typical growing environments of possible CCF systems in the boreal forests of northern Sweden, and (ii) attempts to identify ways in which the environment can be moderated and plant material can be appropriately used to ensure cost-effective regeneration in CCF systems. One of the main hypotheses addressed is that in the examined shelterwood systems seedling growth is affected by both above- and below-ground competition, but the solar radiation regime is the main determinant. The methods used and results obtained have been reported in five papers, designated Papers I to V.

More specifically, the objectives of the studies presented in Papers I and II were to quantify the effects of stand stem density (SSD), orientation and distance with respect to shelter trees, and fertilisation, on the establishment and growth of direct-seeded and planted *P. sylvestris* (*Pinus sylvestris* L., Scots pine) and *P. abies* (*Picea abies* L. Karst., Norway spruce) seedlings.

The specific objectives of the study described in Paper III were to analyse the growth of *P. sylvestris* and *P. abies* growing in identical soil conditions (i.e. soil with the same nutrient status, with or without elimination of competition from surrounding vegetation; or identical soil preparation) under shelterwoods with the same basal area but with differences in stand stem and canopy structure.

The objectives of the studies presented in Papers IV and V were to qualify and quantify, in relation to the solar radiation regime, the establishment and growth of *P. sylvestris* and *P. abies* (IV), and *Betula pendula* Roth. (silver birch), *Populus tremula* (aspen), *Larix sibirica* (Siberian larch), and *Abies lasiocarpa* (subalpine fir) planted in the experimental design of a Chequered-Gap-Shelterwood-System (CGSS) with 0.135 ha gaps under a shelter of pine forest. Four specific questions were addressed. Firstly, what are simulated patterns of solar radiation like in this kind of CGSS (IV)? Secondly, what are the light-related effects of within-gap position on the establishment and growth of *P. sylvestris* and *P. abies* (IV)*?* Thirdly, are there significant effects of distances from forest edges and species on the survival and biomass allocation of seedlings (V)? Finally, can tree species with presumably different solar radiation requirements for growth act as indicators of environmental conditions for establishment in the field (V)?

Material & methods

Study sites

The experiments were performed in the two experimental forests of Vindeln (Svartberget 64°14'N, 19°46'E; Kulbäcksliden 64°09'N, 19°36'E) 60 km NW of Umeå, in the boreal forest of northern Sweden (Figure 2). The two sites considered in Papers I and II (one on a north-facing slope and the other facing south) were dominated by *P. abies* with a vegetation cover dominated by *Vaccinium myrtillus* L. on moist podzolic soils with textures of loamy sandy till. The site considered in Paper III was originally a mixed coniferous forest (mainly *P. sylvestris*) with vegetation cover dominated by *Vaccinium vitis-idaea* L. on a mesic podzolic soil with a texture of sandy silty till. The experiments described in Papers IV and V were performed at two sites dominated by *P. sylvestris* with vegetation cover in both cases once again dominated by *Vaccinium myrtillus* L. on podzolic soils with textures of sandy till. The site characteristics, and the climate conditions during the years of the experiments, are further described in Papers I (Tables 1 and 2), III (Tables 1 and 2), and IV (Tables 1 and 2).

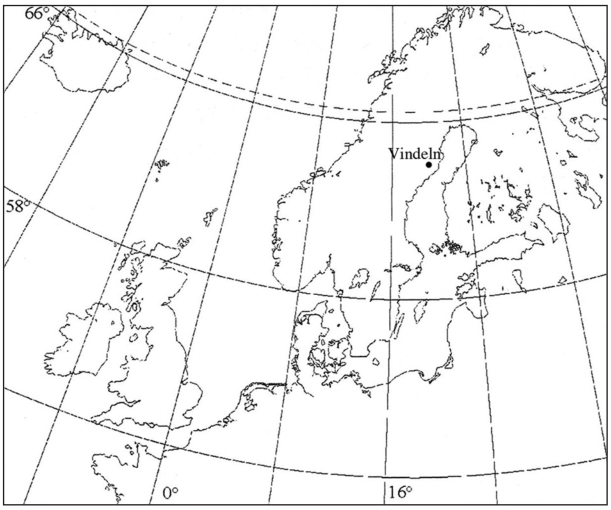

Figure 2. Location of Vindeln, and Vindeln Experimental Forests, Sweden.

Figure 3.View from the east corner of one of the gaps in the older stand (IV,V).

Experimental designs

Paper I and II: Three different types of stands were created at each site, designated SSD 500 (~500 stems/ha, i.e. uncut forest), SSD 150 (~150 stems/ha, i.e. thinned forest or shelterwood) and SSD 0 (clear-cut). The same experimental design was applied at both sites/slopes (Figure 1, I; Figure 1, II). Five shelter trees were selected in SSD 500 and SSD 150. In SSD 0, the locations of two hypothetical trees were marked. Two opposite blocks were delimited in the north-south direction from each selected (or hypothetical) tree. In each block, two sets of six parcels (each 40 × 100 cm) were marked at distances of 0.5, 1, 1.5, 2, 4 and 6 m from the shelter tree. Each parcel was divided into two subparcels (I). Seedbeds were prepared using two kinds of soil preparation (HuMinMix, a mixture of humus layer and mineral soil ground to a fine texture; and bare mineral soil) randomly allocated to each subparcel. Micropreparation was done manually before sowing using a tool with 10 adjacent inverted square pyramids to make indentations in the seedbed to improve capillarity and thus seedling emergence (Winsa & Bergsten, 1994). Ten seeds each of *P. sylvestris* and *P. abies* were sown in each subparcel (I). In each parcel four seedlings, two of *P. abies* and two of *P. sylvestris*, were also planted at least 20 cm apart (II). Furthermore 15 pairs of naturally regenerated *P. abies* seedlings/saplings of three different height classes (<0.5 m, 0.5-1 m, and >1 m; five pairs of each class), were selected in SSD 500 (II). From each pair of parcels at each specific distance and in each direction from the selected (or hypothetical) shelter trees, one was randomly chosen to be fertilised. Fertilisation was performed every other week during June, July and August for the years of the specific experiments. A water solution of N, P and K (10 mM N) was showered onto the seedlings, giving a total amount of at least 0.09 g of nitrogen per season and direct seeded seedling (I). Naturally regenerated seedlings and saplings (one of each pair) were also fertilised, with the same fertiliser and technique. The total amounts of nitrogen provided were 0.56 g per seedling in 2001 and 0.34 g of nitrogen per seedling in 2002-2004 for the planted seedlings, and for the naturally regenerated seedlings and saplings in 2001 and 2002-2004: 2.24 g and 1.34 g for <0.5 m seedlings; 4.48 g and 2.73 g for 0.5-1 m seedlings; and 6.72 and 4.20 g for >1 m saplings, respectively (II).

Paper III: At the experimental site three different plots of about 100x100 m were established. One was clear-cut, while the other two were selectively thinned so that the basal area was reduced to approximately 50% of the original value. One was thinned from above and one from below, to create two markedly different shelterwoods. Thinning from above created a multi-layered stand of *P. sylvestris*, *P. abies* and deciduous trees (mainly *Betula*) of different sizes (a multi-layered shelterwood, MLS), while thinning from below resulted in a shelterwood stand of large *P. sylvestris* (a single-layered shelterwood, SLS). The same pattern of shading on the forest floor provided by the single layer shelterwood was also created in a 50 m^2 circular area in the clear-cut area, by hanging partly transparent "baskets" made from 20 cm wide shading bands wound round a cylindrical iron framework from 17 poles, which were placed in a parabola facing north with several baskets on the south-facing poles to ensure shading at all solar heights during the growing season (Figure 1, III). This "artificial" single-layer shelterwood shading area in the clear cut area was created to solely simulate the shading effects of the SLS, i.e., this treatment was intended to create shading like that provided by older trees but without any root competition. *P. sylvestris* and *P. abies* seedlings were exposed to these treatments in three trials. In Trials 1 and 2 seven seedlings of each species were planted in 10 2x2 m and 0.5 m deep pits, filled with topsoil from a farm field, in the clear cut, MLS and SLS. Seven of the pits in the clear-cut and six pits in each of the MLS and SLS, were lined with a net that was impenetrable to roots. In addition, one 3x3 m pit, in which 24 seedlings (12 of each species) were planted, was created in the artificial shading area of the clear-cut. In Trial 3 *P. sylvestris* and *P. abies* seedlings were planted in nine 2x2 m parcels in each of these forest stand treatment areas, with seven seedlings of each species per parcel, after manually preparing the soil with a mattock.

Papers IV and V: The age (and therefore height and radiation regime) of the stands at the sites differed, one being 30 and the other 50 years old (hereafter referred to as the younger and older stand, respectively; Figure 3). A so-called CGSS felling design was applied, giving two dimensional stands with clear-cuts (gaps) and intact areas in a chequered pattern of rectangles (Figure 1, IV). An area of 90 x 90 m was divided into six chequers each of 30 x 45 m, three of which were selected to be gaps and three to be forest areas/shelterwoods. Outside the 90 x 90m square, a buffer zone was established with 14 further blocks of the same size and in the same pattern as within the square. The gaps and shelterwoods were located in a rectangle, so that each gap was surrounded by shelterwoods. The first chequer was randomly chosen to be gap or shelterwood. In each gap (within the 90 x 90m area) there were nine subblocks (10 x 15 m), each of which contained six parcels (5 x 5m). *P. sylvestris* seedlings were planted in three of the six parcels and *P. abies* seedlings in the remaining three parcels, nine seedlings in each parcel (Figure 1, IV). In addition, in the same kind of system *B. pendula*, *P. tremula*, *P. sylvestris*, *L. Sibirica*, *A. lasiocarpa*, and *P. abies* seedlings were planted at the edges between gaps and forest/shelterwood (0 m) and at two different distances (-7.5 and -15 metres) into the gap and two distances (7.5 and 15 metres) into the forest (Figure 1,V). This was done along three different edges (blocks), each species being planted in a cluster of nine seedlings at each selected distance along six transects between gap and forest in each block. At each site, close to the experimental area, control parcels were also established in a clear-cut area. The clear-cut control contained 36 parcels (5 x 5 m), and nine plants of each species were planted in each parcel, giving a total of six parcels of each species (IV,V).

The experimental designs are more precisely described in the cited papers.

Inventories

Mortality/survival and growth

During the inventories, the height of the seedlings was measured from the root scar/soil surface to the tip of the terminal bud (I-V), and the length of leading shoot was measured as the current year growth of the apically dominant shoot to the tip of the terminal bud (II-V), at the end of each growing season. In the study described in Paper I all emerged or surviving seedlings were recorded, as well as injury and mortality due to predation, frost heaving, physiological and mechanical damage, and mortality due to unknown causes. In the studies presented in Paper II and III the seedlings' status was graded depending on physiological (water stress, frost, fungi) or mechanical damage (mainly browsing), and for Paper IV and V injury (three different levels depending on how much of the seedling was affected) and mortality due to frost heaving or other causes of mechanical or physiological damage were recorded.

Seedlings were destructively sampled for biomass measurements, by cutting them at the soil surface and divided them into three different fractions (stem, twigs, and leading shoot) after the abovementioned characteristics had been measured. Roots of a smaller number of randomly selected seedlings were also harvested (II; Trial 1, III). To estimate their dry masses the different fractions were dried at 85°C for 48 hours before weighing. The biomass data were further used to transform height measurements to biomass estimations (Trials 2 and 3, III).

Biomass estimation by image inventory (V)

An approach for estimating biomass based on image inventories was applied in the study reported in Paper V. Photographs were taken horizontally of a representative seedling from each cluster at -15, 0, and 15 metres from the edges in two randomly chosen blocks, in each of the two stands, from a distance of 1.5, 2, or 2.5 metres (depending on the seedling size) in front, facing south, (in total 72 photographs), using a tripod-mounted Nikon Coolpix 4500 digital camera at 2272x1704 resolution, with high quality definition. Photographs were taken on overcast days, to avoid shadows, using a light blue background, and later automatically processed using WinCAM^{TM} (Regent Instr., 2007), which enables images to be analyzed according to group colours in order to distinguish objects from the background. The "biomass" referred to in this paper is the silhouette area of needles/leaves, which was shown to be correlated to root collar diameter, allowing estimates of the silhouette area for all nine seedlings in each cluster at the time of the image inventory to be estimated from root collar diameter measurements.

Fish-eye photographs (I, II)

The light environment in each of the SSD's in the experiments described in Papers I and II was characterised by the total site factor (TSF), i.e. the relative amount of incidental (direct + diffuse) photosynthetic photon flux density (PPFD) that penetrates below the canopy during a specified period of time. To do this, fish-eye photographs were taken during totally or partly overcast days (Figure 4) at distances of 1.25 and 5 m north and south of the selected shelter trees. In SSD 0 a photograph was taken at the point of each hypothetical shelter tree (and thus two photographs from each slope). The photographs were analyzed using WinSCANOPY™ software (Regent Instr., 2005) with the pixel classification in grey scale and the time for growing season set as June 1-September 30.

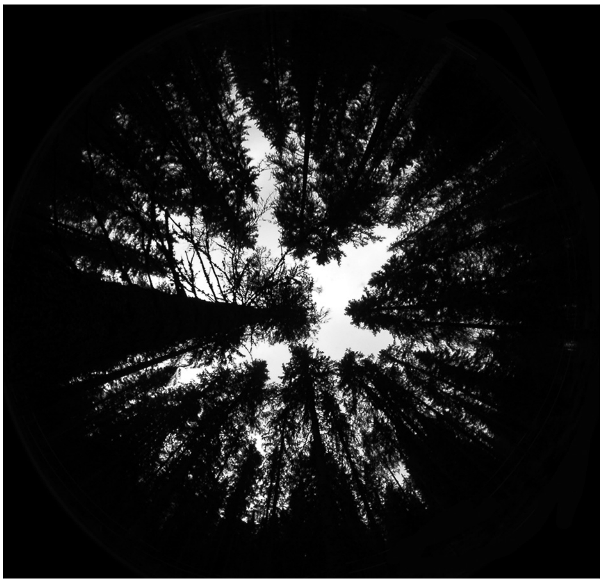

Figure 4. A fish-eye photograph taken under optimal overcast weather conditions.

Radiation simulation model (IV)

The radiation simulation model presented in Strand et al (2006) was used in Paper IV, but with site-specific adaptations, to simulate the solar radiation in the CGSS, assuming that the surrounding shelter trees would affect the radiation regime of the seedlings in the gaps. Measurements of solar radiation (PPFD) above ground vegetation during the growing season of 2009 were used to validate the radiation model. The simulation model computes the solar radiation reaching the surface of the earth by calculating the extraterrestrial solar radiation, taking the atmospheric attenuation into account, and determines the diffuse sky radiation. The sun altitude alone is used to calculate the clear sky diffuse radiation. Based on date, time and latitude, the model calculates the clear-sky direct and diffuse radiation above the shelterwood canopy. Results obtained by this method for estimating global radiation agreed well with observed data from the reference climate station at the Svartberget Experimental Forest (64°14'N, 19°46'E) and generated appropriate background data for the CGSS simulation.

A subroutine was then used to simulate the tree shading and estimate the daily irradiance at the selected points in the CGSS (Granberg, 1988). The shadow of each shelter tree was projected onto the ground surface using the sun's position to determine its length and direction. The simulated pine trees were modelled as a 'cone-on-a-stick', the cone consisting of 35 whorls each with four branches and additional outer twigs, thus producing shade similar to partly transparent tree crowns. The simulation model uses the shelter tree positions to plot the shade cast, with black pixels inside the predefined white square representing the shelterwood area on the screen. The resulting plot of the tree shadows on screen was analyzed by determining the status of each pixel within the plot area. The simulated solar radiation for a specific point was based on the mean value of nine pixels; the central pixel and the eight adjacent pixels. The ratio between the daily irradiance at each seedling position and the above-canopy clear-sky irradiance was defined as the solar radiation transmission. Further details of the simulation subroutine are presented in Paper IV.

Statistics

Analysis of variance, using the GLM procedure in MINITAB Statistical Software (2006), was applied (for each site since there were generally significant between-sites differences), to assess the main and interaction effects on the seedlings' mortality, survival and measured growth variables of: SSD, orientation and distance in relation to tree, soil preparation, and fertilisation, by species (I, II); gap, sub-block, and other subdivisions of gap, by species (IV); block, species, and distance from edge (V); for each trial, stand treatment, and net lining, by species (III).

Prior to running the tests, data were tested for homogeneity of variance (using Levene's statistic). Due to predation/browsing growth could not be analyzed for all combinations of species and factors. When interactions were not significant, they were excluded from the models. When significant effects were found (at the 0.05 probability level), Tukey's multiple comparison test was used to test differences between treatments.

The height growth of naturally regenerated seedlings was analysed using MINITAB's Paired-sample t-tests with a confidence interval of 95% for mean differences (II). The seedlings in the artificial shelterwood (Trial 1) were compared separately to the seedlings in the SLS (Trial 1), with biomass as dependent variable, using MINITAB's Two-sample t-tests (Minitab, 2006; III). The height growth of seedlings in the centre of the gaps (subblock 5/-15 m) was compared to the height growth of seedlings in the control parcels of the clear-cut, once again using MINITAB's Two-sample t-tests with a confidence interval of 95% for mean differences (ibid; IV,V). The height growth of seedlings in subblocks 3 and 7 was compared using MINITAB's Paired-sample t-tests (ibid; Figure 2, IV). The data presented in the following sections are means, and both between-treatment and between-species differences mentioned are significant at the 0.05 probability level unless otherwise stated.

Results & discussion

Growing conditions for a seedling in relation to distance from shelter trees (I, II, V)

In the same way as a natural forest has a distribution of gap sizes, a managed forest subjected to silvicultural treatments can have a gap size distribution. Habitat conditions vary among gaps, within gaps, at gap edges, and within the forest stand matrix (Coates & Burton, 1997). In forests, there are very complex microclimatic variations and interactions. Large openings are exposed to a higher amount of shortwave radiation, more extreme changes in temperature between night and day, higher ground temperature and greater wind speeds than a closed forest (Geiger, 1995). The microclimate and local climate affect seedlings and trees as well as forest stands both directly and indirectly very strongly, and the chances for survival and growth of any individual depend on the local climatic conditions.

Average data obtained from the stands indicate that the light environment within stands of the same stand density on the two slopes was very similar. However, it clearly differed substantially between SSD's; <20%, 40% and 80% of the PPFD above the canopy was transmitted in SSD 500, SSD 150 and SSD 0, respectively (Figure 1, I). No significant differences were found between the different orientations or distances with respect to tree. Accordingly, orientation and distance with respect to tree generally had little effect on growth for this plant material and in these SSD's (I, II). In contrast, at sites with lower SSD's than 150, and in potentially less fertile pine forests, Björkman (1945), Strand et. al. (2006) and Elfving and Jakobsson (2006) have found positive correlations between the distance to the nearest shelter tree and growth of seedlings/saplings and trees, respectively.

Emergence

The establishment and growth of seeded seedlings were highly dependent on species and SSD (I), in accordance with expectations since the shade tolerance of *P. abies* and *P. sylvestris* differs, but both species benefit from the increased radiation provided by canopy gaps (de Chantal *et al.*, 2003b). On the North slope, the emergence was highest (49.5%, i.e. 49.5 seedlings per

100 germinable seeds for *P. sylvestris* and 44.2% for *P. abies;* Table 4, I) in SSD 150. In contrast, on the South slope the conditions in SSD 0 most favoured emergence of *P. sylvestris* (41.3%;Table 4, I), whereas for *P. abies* there was no significant difference between SSD 0 and SSD 150 (27.8% versus 30.1%, respectively; Table 4, I). These findings differ somewhat from observations by Granhus et al. (2008) and Hanssen et al. (2003) that clear-cut treatment is less favourable for the emergence of naturally regenerated *P. abies* seedlings, possibly due to poorer seed availability, more extreme conditions, and greater soil erosion, than shelterwoods of both high and low residual basal areas. Further, for *P. abies* on the South slope, emergence rates tended to be highest (ca. 30-35%) at positions at least 1.5 m away from trees on the north slope, and lowest (ca. 20%) at distances between 1 and 2 m on the south side of trees. The emergence of *P. sylvestris* on the South slope was higher on the north side of trees (31.5%) than on the south side (27.7%) and the emergence at points 1 m away from trees was lower than the emergence 4 and 6 m away (24.6 %, 33.9%, and 33.4%, respectively; Table 6, I).

The HuMinMix soil preparation method favoured seedling emergence in accordance with previous research (Winsa, 1995a). In SSD 150 on the South slope, the emergence of *P. abies* was about 40% higher on HuMinMix plots (35.1%) than on mineral soil (25.1%; Table 5, I), while the emergence of *P. sylvestris* on the North slope was much lower on mineral soil than on HuMinMix in SSD 500 (19.4% and 32.5%, respectively; Table 5; I), and on the South slope the emergence of *P. sylvestris* was also lower on mineral soil (28.5%) than on HuMinMix (34.8%), irrespectively of SSD. For direct seeded *P. abies* (on the North slope), damage by frost heaving was highest on mineral soil in SSD 0 (14.3%), in accordance with reports by Goulet (1995), and for *P. sylvestris* frost heaving damage was highest in SSD 0, irrespective of soil preparation (15.6%; Table 7, I). Consequently, de Chantal et al. (2007) suggest that to reduce the risk of frost-heaving damage, shallow soil preparation and smaller gaps should be used. Predation was found to be lowest in SSD 500 on both slopes (North slope 27.4% and South slope 38.9%; Table 8, I).

Growth and fertilisation effects

The only fertilised seeded seedlings that were significantly taller (ca. 20%) than non-fertilised counterparts after three years were *P. abies* seedlings on the North slope (I). Among planted *P. abies,* fertilised seedlings in SSD 0 grew the most (22.2 cm on the North and 34.2 cm on the South slope; Table 2, II). Fertilisation had no effect on height growth of planted *P. sylvestris*, but their growth clearly increased (from <20 cm to >50 cm) with decreasing SSD (II). The naturally regenerated seedlings/saplings in the different height classes showed no response in height growth to fertilisation (II). They grew in SSD

500 and if they had been subject to growth release they might have responded differently. The effect of growth rate prior to release on the magnitude of release responses varies among trees of different diameters and species, but the slowest growing and smallest individuals of all tested species (*Thuja plicata, Tsuga heterophylla* and *Abies amabilis*) all displayed the most intensive releases in a study by Stan & Daniels (2010).

Planted seedlings in SSD 0 had the greatest biomass of branches and leading shoot (green biomass; II). On the North slope, fertilisation had an effect on *P. sylvestris* in SSD 0, with fertilised seedlings having greater green biomass (62.6 g) than non-fertilised seedlings (39.7 g; Table 4, II). In SSD 0 on the South slope, fertilised *P. abies* seedlings had greater green biomass (40.4 g) than non-fertilised seedlings (23.6 g; Table 4, II). For *P. sylvestris,* seedlings in SSD 500 had the highest fraction of roots (ca. 20%; II). For planted seedlings, comparing the results of dry mass of leading shoot with those of height growth showed differences between species and SSD's (Figure 5, II). For planted seedlings, greater between-SSD differences were found in the dry mass of leading shoots than in height growth (Figure 5, II), most extremely among *P. sylvestris* seedlings, for which the dry leading shoot mass in SSD 500 was only 3% of that in SSD 0, while for height growth the corresponding difference was almost 30%. These findings indicate that height growth is not a good measure of the overall growth of seedlings, especially under shelter (i.e. in CCF systems). The conclusion drawn in Papers I and II is that inadequate light conditions in SSD 150 and SSD 500 made the seedlings in almost all cases incapable of responding to fertilisation. This finding is consistent with observations by other authors, for instance Mitchell (2001), who concluded that retention of 25% of the preharvest overstorey stand structure can limit the early growth of regenerating montane conifer seedlings, presumably as a result of a 47% reduction in available light and not as a result of reduced nutrient availability.

Growth and effects of seedling light tolerance

Seedling survival in the younger stand examined in the study described in Paper V was generally high in gaps and lower in the forest/shelterwood. The conditions in central parts of gaps did not limit seedling height growth, compared to those in a clear-cut, since growth was never lower in gaps, but there were effects on height growth of both distance from edges and species in both stands (V). In the older stand, for example, there was generally greater estimated biomass in gaps than at the edges and in the forest (586.4 ± 93.5 versus 203.8 ± 22.3 and 121.3 ± 24.1 cm^2, respectively; V). In both stands *A. lasiocarpa* proved to be a tolerant species, with low overall mortality rates (maximum 5%; V). In agreement with documented differences in responses between the light-demanding *P. sylvestris* and the less light-demanding *P. abies*, *P. abies* seedlings also had relatively high survival rates across distances and in both stands, while the survival rate of *P. sylvestris*, in contrast, was at its lowest in the forest of the younger stand (Figure 2, V) and overall second lowest in the older stand (67.9%), possibly due to combined effects of low light and predation (de Chantal et al. 2003b; Dehlin et al. 2004; V).

In the younger stand *L. sibirica*, which is a fast-growing conifer species, displayed the greatest height growth of all tested species, but *P. sylvestris* grew more than *L. sibirica* in the older stand (26.2 versus 21.3 cm; V). The height growth of *B. Pendula* and *P. tremula* was good overall, in accordance with their known attributes as rapidly growing, light-tolerant, pioneer species (Delagrange *et al.*, 2006), while the height growth of the more light-intolerant, secondary species of *A. lasiocarpa* and (particularly) *P. abies* was relatively weak. Despite low survival rates of deciduous species in the gaps, due to predation/grazing, they generally grew well in height (V). In the younger stand, *L. sibirica* had significantly greater estimated needle biomass in the gap than *P. abies*, which had low biomass (Figure 5; V). Furthermore, the biomass of *A. lasiocarpa* in the forest was equal to that of *P. abies* in the gap, the biomass of *P. abies* did not differ between distances from the edge, and *P. sylvestris* in the

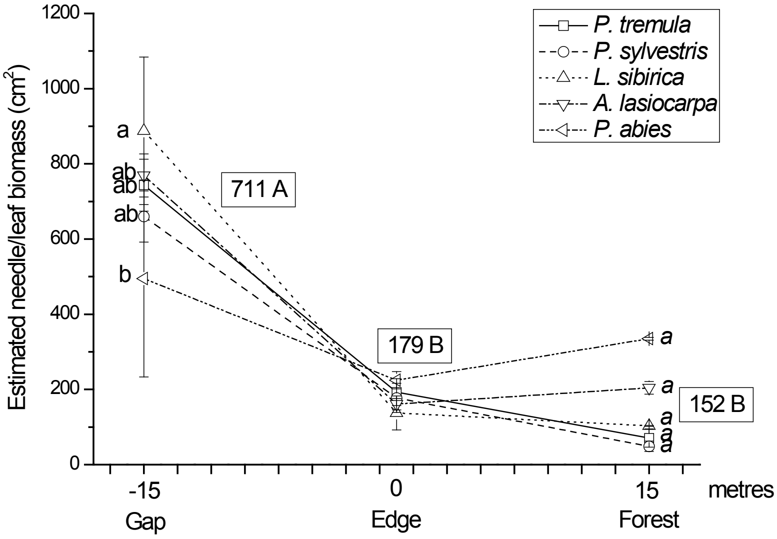

Figure 5. Estimated needle/leaf biomass (cm^2) of *P. tremula, P. sylvestris, L. sibirica, A. lasiocarpa*, and *P. abies* seedlings in the gap (-15 m), at the edge (0 m), and in the forest (15 m), of the younger stand. Different lower case letters indicate significant differences among species within distances (italics for mean values in the forest; Tukey's test, $p \leq 0.05$); different capital letters indicate significant between-distance mean differences. Error bars denote the standard error of estimated biomass.

gap had equal needle biomass to *P. abies* in the forest (Figure 5; V). For the last mentioned comparison, once again most likely there was an effect of predation pressure in the clear-cut. The lack of between-distance to edge differences in *P. abies* biomass further confirms its light-intolerance, which was also evident when the ratios between estimated biomass of seedlings in the forest and the gaps in these three species were compared. This ratio was highest for *P. abies* and second highest for the intermediately tolerant *A. lasiocarpa* (Figure 4, V). In both stands, biomass and height growth generally had the same relationships to distance from edges, decreasing at the edge and remaining low in the forest. This could be due to PPFD levels being too low for satisfactory growth even at the edges between gap and forest, for all species. Those findings are concordant with results from North America presented by Ye and Comeau (2009), who found that height growth of edge trees of *Populus tremuloides* Michx. was not significantly different from that of trees within the surrounding stands.

Creating optimal growing conditions at stand level (I, II, III, IV, V)

Regeneration under shelter versus in gaps

Among the seeded seedlings, *P. abies* seedlings on the North Slope were most successful, but nevertheless only 8.8 of these seedlings were present after four years, out of 23.8 that emerged per 100 germinable seeds (Figure 4, I). The clear patterns observed for height growth of planted seedlings in relation to SSD, with *P. sylvestris* in SSD 0 having the highest growth, is not surprising considering that *P. abies* is shade-tolerant and *P. sylvestris* shade-intolerant (Figure 3, II). Habitat conditions are important and play major roles in determining the success of regeneration (Coates & Burton, 1997), but there have been few attempts to assess stand matrices in terms of suitability for tree establishment and growth. Nevertheless, the following relevant observations have been reported. Bergqvist (1999) studied *P. abies* (35 to 37 years old at the establishment of the trial) growing under a shelter of *Betula pubescens* Ehrh. and *Betula pendula* Roth. with two different stem densities (300 and 600 stems per ha), and found that compared to *P. abies* growing on a clear-cut height growth did not significantly differ. However, wood volume yield was consistently higher, and diameter growth was initially faster, on the clear-cut than in both shelterwoods (between which there were no significant differences in these variables). He concluded that the lack of response in height, together with increased diameter giving a lower slenderness index in the clear-cut, was mainly due to light being the prime limiting factor. Bräker and Baumann (2006) concluded, after examining trees bordering several rectangular slots cut for regeneration, that 100-year-old, sub-alpine *P. abies* stands still seem to be capable of reacting to sudden changes in light availability. The germination, survival and growth of shade-tolerant and shade-intolerant tree species have often been correlated with gap size. Light conditions at ground level throughout forest stands are directly related to gap size, shape, canopy height, and latitude, and since light availability can vary sharply over short distances within gaps, the position within gaps strongly influences the physiology and growth of any individual tree seedling (Wayne & Bazzaz, 1993). Seasonally integrated light transmission at the centre of a 24 m diameter gap in a homogenous, 10 m tall birch stand of North America is about 60%, while at the centre of a 12 m gap it is 40% (Comeau *et al.*, 1998). In a study of five conifer species (*Thuja plicata*, *Tsuga heterophylla*, *Abies lasiocarpa*, hybrid spruce, and *Pinus contorta*) Coates (2000) found that growth of all five species in gaps greatly increased with increases in gap size from small single-tree gaps to about 1000 m^2, but there was little further change in growth with further increases in gap size up to 5000 m^2. In large and medium-sized gaps (301-1000 m^2), the largest trees of all species were found in the middle gap position and for most species there was little difference in growth between the north and south positions. In the smaller gaps, as well as in the forest understorey, total size and growth rates were almost identical for all species.

Effects of nutritional status in different stand treatments

In Trial 1 (III), when planted in soil of good (and equal) nutritional status, the height growth of both *P. sylvestris* and *P. abies* was greatest in the clear-cut compared to the two shelterwoods. However, in Trial 2 (following depletion of nutrients after growth of the seedlings in Trial 1, but with otherwise similar below-ground conditions) *P. abies* grew more slowly in the MLS (*P. sylvestris* growth was not assessed in the second trial) (III). Thus, with good supply of nutrients, the height growth of seedlings seemed to be less affected by the differences in PPFD levels between the MLS and SLS. Furthermore, in both trials the height growth of *P. abies* was positively affected by the pit being lined with a net (III). Comparisons of the height growth and biomass of the species also showed some intriguing relationships. As for height growth of *P. abies* in Trial 2, needle and root biomass in both trials were greatest in the clear-cut, less in the SLS, and least in the MLS, except for *P. sylvestris* in Trial 1, for which biomass (as for the height growth of both species in Trial 1), was greatest in the clear-cut but did not differ between the MLS and SLS (Figure 2, III). Once again *P. sylvestris* responded more sharply to reduced transmission of PPFD, since its growth was dramatically (85%) lower in the MLS and SLS than in the clear-cut (III). In a 7-year period after harvest, Granhus and Brække (2001) studied the nutrient status of *P. abies* stands subjected to different levels of overstorey removal, and found that sapling needle weights generally increased with harvest intensity whereas no effect of foliage nitrogen status on needle

Figure 6. An aerial photograph of a Chequered-Gap-Shelterwood-System (the younger stand, IV and V). Photograph: Olle Hagner.

weights was detected. Their results illustrated that sufficient nitrogen supply is a key factor for the ability of advance regeneration to utilise the improved light conditions associated with overstorey removal. The needle biomass values of both species in Trial 3 (in which soil was prepared with a mattock) were also low compared to values in Trials 1 and 2, considering that the seedlings in Trial 3 had grown for twice as many years before the biomass measurements (III). *P. sylvestris* seedlings had very little needle mass in both the MLS and SLS, possibly as a result of growing in shade, and exposure to belowground competition, for six years, compared to the three years for the seedlings in Trials 1 and 2, respectively (III).

P. abies had very high survival rates in all trials and all forest stand treatments included in the study described in Paper III, while *P. sylvestris* generally had a high survival rate in the clear-cut, and lower rates in the shelterwoods. In Trial 1 there was no difference in survival rates of *P. sylvestris* between the MLS and the SLS, which appeared to be due to the good nutritional status of the soil, since the MLS was the least favourable of the habitats for growth, when seedlings were grown in the local soil after manual soil preparation (Trial 3; III). Both the needle and root biomass of both species was greatest in the clear-cut when they were grown in identical, good soil (*P. sylvestris* 63 and 14 g, respectively; *P. abies* 34 and 12 g, respectively; Figure 2, III).

With those soil conditions, there was also no difference in growth, at least for *P. sylvestris,* between the multi-layered and single-layered shelterwood. With increased belowground competition, seedlings grew more slowly in the MLS compared to the SLS. As Tamm concluded 1954, by studying forest fertilisation in Germany and Sweden, fertilisation can be a way to enhance regeneration in shelterwoods. Supported by the comparison between seedling growth patterns in the artificial shelterwood and SLS, light conditions to a large extent explained differences in seedling growth between stand treatments in the study of Paper III.

Silvicultural systems allowing flexibility in resources

The silvicultural systems of small group selection (cutting in 18 m circles) and strip-cutting (cutting in 18 m wide strips) in northern latitude forests provide 55% and 68% of total growing season solar radiation, respectively, which allows sufficient light to penetrate to the ground surface to ensure the development of spruce seedlings (Grossnickle, 2000). One method that has been used in Britain (Mason & Kerr, 2004) is felling small groups of trees in 0.1 to 0.5 ha areas (group shelterwood) and replanting with desired species, but taking advantage of natural regeneration if, and when, it appears. A problem with this system in Britain has been rapid vegetation colonisation, but in the northern parts of Scandinavia a system like this would probably give better results as the fertility of stands is usually rather low. According to Streit et al. (2009) the creation of slit-shaped gaps is a successful procedure for promoting *P. abies* regeneration in the upper montane and subalpine belt of the northern intermediate Alps and it also helps to preserve protection forests and their goods and services for coming generations. Ciancio et al. (2006) conclude that the description and re-appraisal of traditional silvicultural systems, which have been developed and applied in diverse environments using various techniques, which are often quite different from well-established silvicultural methods, can make important contributions to searches for ecologically, economically and socially sustainable ways of managing forests.

A way to regenerate forests that could exploit the benefits of shelter trees and at the same time create the desirable conditions of a clear-cut, may be a system in which forest gaps are formed within a shelterwood as in the CGSS (IV). The optimum radiation regime and moisture conditions for the species of concern can be met by deciding shelterwood density, gap size and shape, as well as within-gap position. This can provide secure regeneration, without necessarily reducing regeneration growth compared to growth in a clear-cut. Further, such a system can be designed to be applicable in conventional forestry, with gap dimensions (e.g. 20-40 × 30-60 m) that can be cut cost-effectively by a conventional harvester working diagonally through a chequered pattern.

Further, seeding or planting could be used with the advantages of not being reliant on natural regeneration and the ability to introduce desired species and genotypes that may not be present in the stand. Light-intolerant species can be regenerated in areas of the gaps with relatively low light levels, while light-tolerant species can be advantageously regenerated in areas with relatively high light levels (IV,V).

In the study reported in Paper IV on regeneration in a CGSS, preliminary simulations of solar radiation regime were made for both the younger (Figure 6) and older stands. In the younger stand (of lower tree height) the radiation regime was almost homogenous within the gaps. In the older stand, in contrast, on a clear sky day with a simulated global radiation of 32.6 $MJm^{-2}day^{-1}$, differences were found between central and both south-facing and north-facing parts of the gaps, with levels of transmission ranging from around 30% in the south-west parts up to 90% in the central and more south-facing parts (Figure 4, IV). From calculations based on the simulation, transmission values exceeded 75% on about 18% of the ground floor area in the CGSS of the older stand. That 18% of the ground floor area was in the central parts of the gaps, extending up to ca. 7.5 metres from the shelter/forest edges, a distance at which the results presented in Paper V show that seedling growth was still good. Overall survival rates of seedlings in the gaps were very high. The results from the radiation simulation model were related to seedling height growth by seedling positions within gaps. Notably, *P. sylvestris* seedlings in the older stand showed significantly larger height growth in the south-facing subblocks than the north-facing subblocks (37.3±1.1 versus 30.8±1.4 cm, respectively; Figure 5, IV). In the younger stand there were no corresponding significant differences, but already a strong tendency for growth of *P. sylvestris* to be stronger in the south-facing subblocks (33.3±1.7 versus 29.4±1.5, $p=0.092$; IV). In the older stand *P. abies* showed a similar, significant difference in height growth; but only between the most south-facing subblock (subblock 3; Figure 2, IV) and the most north-facing corner (subblock 7; 17.5±7.5 versus 10.4±5.3, respectively; Figure 5, IV). The study of Thiel and Perakis (2009) further supports the hypothesis that light can be the most limiting factor, as their results suggest that increased nitrogen availability in 6-8-year-old silvicultural gaps in young western Oregon forests may be due more to the quality and quantity of litterfall inputs resulting from early-seral species colonizing gaps than to changes in temperature and moisture conditions caused by gap creation. Frelich et al. (2003) found N, and light availability, to have moderate influence on understorey plant community structure, even though the plant species are arranged along N and light gradients. Further, in their studies in old-growth mixed *Pinus resinosa* and *Pinus strobes* forests of North America, they found that variation in N does not exert as strong control over community structure as it does at landscape scale. Both Frelich et al. and Moora et al. stress the importance of disturbance for spatial pattern and species richness, the latter having studied the understorey in boreonemoral forests of Estonia.

The radiation model simulates the conditions of a clear-sky day, in which differences in transmission of solar radiation between stands will be maximal (IV). On cloudy days (with no direct radiation), the radiation regime within the CGSS is much less heterogeneous. The results of Bernier et al. (2001) highlight the importance of diffuse radiation within the canopy, both because of the great efficiency with which it is absorbed by the shoots and the fact that its presence tends to reduce differences linked to the geometry of shoot-light interactions. Gu et al. (2002) further state that diffuse radiation results in higher light use efficiencies by plant canopies, has much less tendency to cause canopy photosynthetic saturation, and its advantages over direct radiation increase with radiation level.

Managing forests for light

CCF formation for regeneration

The key determinants of the gap size and shelter tree density required to ensure that light levels are optimal for the regeneration of specific tree species when creating a CCF system are the external factors nutrition level and sun angle, together with the tree/stand height. If nutrition levels and sun angles were high, while tree height was low, the optimal system would have small gaps and high shelter tree density, since competition from surrounding vegetation could be severe and solar radiation would still be able to reach the regeneration from vertically above. On the contrary, low nutrition level and sun angle together with tall trees, would result in an optimum of large gaps and low shelter tree density (Figure 7).

CCF (CGSS) formation
based on external factors affecting seedling establishment

Nutrition level	Sun angle	Tree height	Gap size	Shelter tree density
High	High	High	Medium	High
		Low	Small	High
	Low	High	Medium	Low
		Low	Small	Low
Low	High	High	Large	High
		Low	Medium	High
	Low	High	Large	Low
		Low	Medium	Low

Figure 7. External factors and the potential formation of CCF/CGSS for optimal regeneration.

System improvements with tools for modelling solar radiation regimes

Promis et al. (2009) found that the transmission of solar radiation was affected in an uneven-aged, evergreen *Nothofagus betuloides* forest of Chile not only by high levels of horizontal and vertical heterogeneity of the forest canopy, but also by the angles of the sun's path. Accordingly, in northern latitude forests, with low sun angles, the orientation of a CGSS/gap presumably affects the solar radiation regime (de Chantal et al. 2003b). Thus, the radiation regime of the older stand would be somewhat altered (presumably resulting in the penetration of more solar radiation into the understorey along the south-facing cut-faces) if the CGSS had a north-south orientation (Figure 6, IV). Using a simulation model, like that applied in Paper IV, the scope for varying the solar radiation regime by modifying the shape of gaps (in addition to compass-orientation) and stem densities of the shelterwood could be explored. Suppose that a system of gaps shaped like triangles, in order to maximize a positive effect of south-facing parts of gaps, was created. Using the same stand stem density as in the older stand (corresponding to a basal area of approximately 30 m^2 ha^{-1}) and roughly the same gap size, and simulating according to the procedure described in Paper IV, about 19% of the ground floor area in a system of triangles pointing south would have transmission values greater than 75% (Figure 8). Turning the triangles through 180 degrees, creating gap triangles pointing north, would result in approximately the same percentage of ground floor area, 17%, having fairly good transmission values for tree seedling growth (Figure 8). Clearly, changing the gap shape from rectangular to triangular would not make much difference to the transmission of solar radiation in this example.

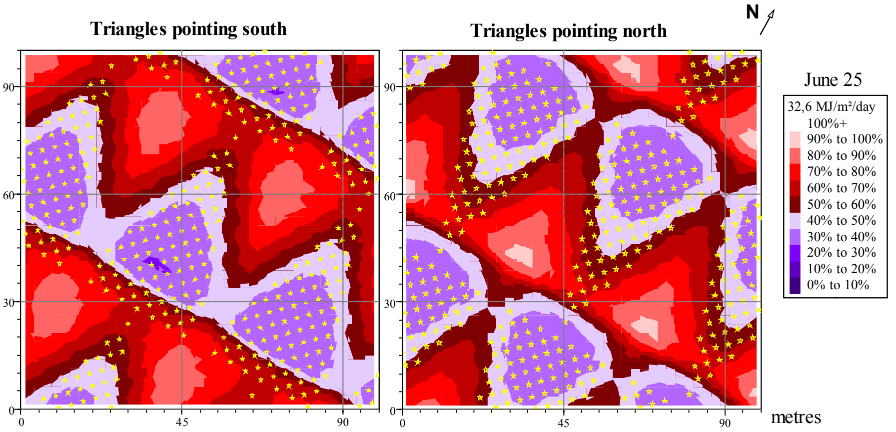

Figure 8. Simulated solar radiation in a CGSS of triangles pointing south (left) and north (right), in percent of above canopy radiation, June 25, 2009.

In contrast, as suggested in the literature (de Chantal *et al.*, 2003b), the area of the system with "good" transmission values increased to 31% when simulating "oval/elliptical patterns" in a north-south orientation, formed by joining pairs of triangles (Figure 9). Since the size of the window of the simulation model is no more than one hectare, these predictions may be over- (or under-) estimates, depending on the precise location of the gaps within this hectare of the system. Nevertheless, this simulation indicates that oval or elliptical formations may provide a way to further develop the CGSS, possibly in combination with different stem densities of the shelterwood areas. In assessments of modified gap shapes their practicability for harvesters must of course also be considered, especially in terms of the size of gaps in relation to boom lengths and the possibilities for creating roads. Clearly, it has to be mechanically possible to release the regeneration and cut the shelter trees at appropriate times, without excessive damage. A study on the spatial distribution of injuries to *P. abies* advance growth after selection harvesting by Granhus and Fjeld (2001) found that frequencies of total injuries varied from 17–76%. Furthermore, the spatial risk of injury depended on interactions between the height and location of saplings, and operational characteristics. Hence, all of these factors need to be considered.

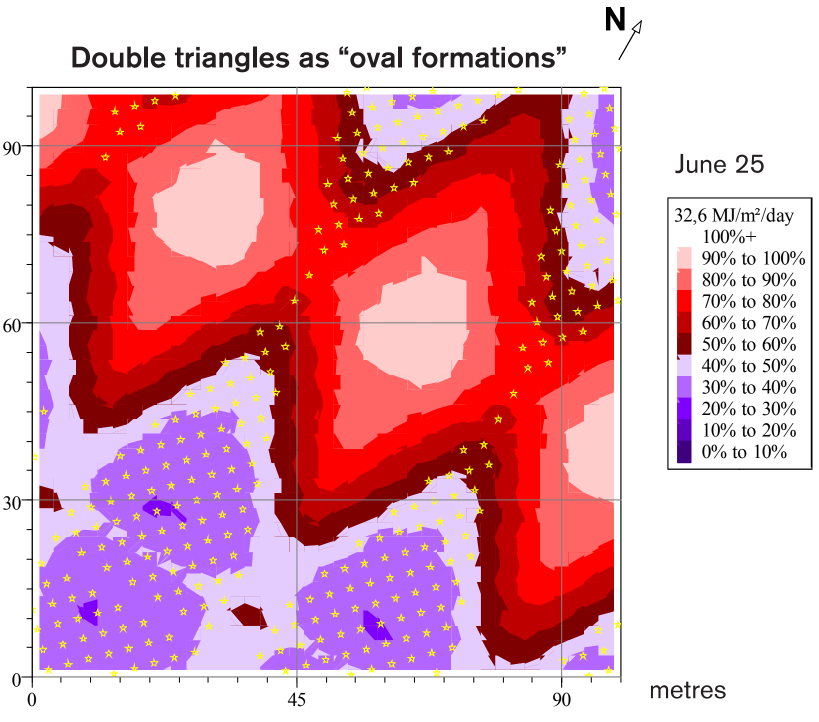

Figure 9. Simulated solar radiation in a CGSS of "oval formations" created from double triangles in north-south orientation, in percent of above canopy radiation, June 25, 2009.

When choosing an approach for modelling the radiation regime in plant canopies, like a three-dimensional landscape radiative transfer model capable of handling two or more vegetation types of varying canopy structure, self-shadowing, and shadowing between canopies, Asner et al. (1998) point out that the absorption of PAR (PPFD) by non-photosynthetic plant components should be accounted for. Astrup et al. (2008) tried to find the optimal level of complexity for a simulation model by comparing forest growth models simulated by the forest simulator SORTIE-ND. They found that functions of intermediate complexity had the best predictive ability; the poor predictive ability of the simplest model was due to poor approximation of the system, while the poor predictability of the most complex model was caused by biased parameter estimates (ibid.). Results presented by Cescatti (1997) indicate that the variability in the radiative fluxes due to shoot architecture is rather limited in comparison with the variability generated by canopy discontinuities. Modern silvicultural treatment programmes, methods of conversion of pure to mixed stands and natural regeneration techniques cannot be tested experimentally before their transfer into practice due to the long period of time required for forests to develop. Models make it possible to reproduce, optimise and modify new treatment variants with the help of a simulator, and evaluate the predicted economic, ecological and socio-economic consequences (Pretzsch, 2009).

Species choice and growth estimations

The study described in Paper V suggests that the requirements of the tree species to be regenerated are an important consideration if regeneration is to be secured by managing forests' light regimes. For instance, satisfactory growth of *B. pendula*, *P. tremula*, *P. sylvestris*, *L. sibirica*, *A. lasiocarpa*, and *P. abies* may require different radiation regimes, since they respond differently to changes in solar radiation (V). The right match of species, with regard to light tolerance, and growing environment will make CCF applicable in a wider range of stand types, as clear-cuts will not be needed to optimize regeneration growth. Biomass estimation of seedlings by image analysis (V) can be further developed into efficient ways of evaluating regeneration success without disturbing the growth (Bloomberg *et al.,* 2008). Use of an appropriate background when taking the photographs, in combination with established models for colour differentiation in analysis software, could enable differentiations of, for example, shoot age.

Retention of trees

As shown in Papers I-V there are advantages of regenerating tree species in CCF systems, but there are also many different reasons for choosing to retain mature trees in a forest stand (Figure 10). Forest ecosystem services, including the existence of certain forest types and their attributes, are renewable social assets, that provide diverse benefits. There is a need to use new paradigms of managing forest ecosystems, together with improved modelling tools, which permit accurate forecasting and systematic evaluation of different management options, based on current information about the forest resource (Gadow *et al.*, 2007). As a CCF system in practical forestry, CGSS could be multifunctional in terms of regeneration, since there are possibilities to create habitats of differing solar radiation levels, and moisture conditions, within the same system. The optimum conditions for specific, not necessarily tree, species of concern can be met, and the tree continuity in itself could favour other ecosystem components, for example tree-living lichen species. A CGSS could also be multifunctional in terms of meeting contrasting needs and demands of society and silviculture, mainly by avoiding clear-cutting.

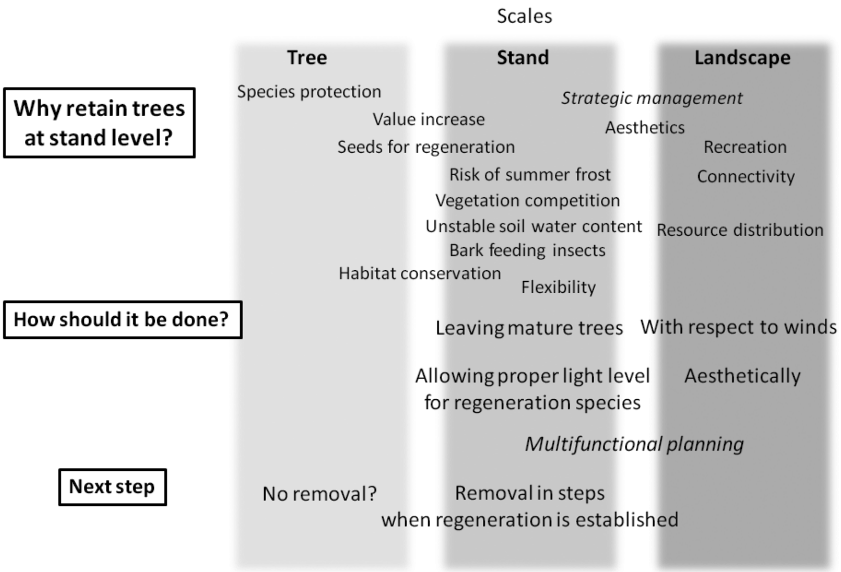

Figure 10. The rationales of CCF with retention of mature trees.

Despite the varying reasons for choosing to retain trees, it is essential to develop practical and economical ways of practicing CCF before implementing the system. According to Price and Price (2008), based mainly on observations of the system in the UK, the extra harvesting costs of group or shelterwood felling are likely to exceed any savings in regeneration costs, but values vary greatly with location and the version of CCF considered. Harvesting techniques are of central importance in practicing alternatives to rotation forestry (Cedergren, 2008). Layered forest stands could be created in various ways, as illustrated by the MLS and SLS examples described in Paper III, but a system like the CGSS could (with the sun angles of the northern latitudes) be both practical and economical with gap sizes suited for conventional harvesters. Regarding biotic and abiotic risks of damage associated with silvicultural systems, Jactel et al. (2009) conclude that forest management is a question of compromises, in which one has to balance risks and benefits not only for every silvicultural operation but also for their possible interactions or cascading effects.

Conclusions

The following general conclusions can be drawn from the studies, conducted in the boreal forest of northern Sweden, underlying this thesis:

1) In the establishment of *P. sylvestris* and *P. abies* plants the general conditions of the stand matter more than the orientation and distance with respect to the nearest tree under a shelter of spruce forest of no less than 150 stems per ha.

2) There are differences in the growing conditions for *P. sylvestris* and *P. abies* between shelterwoods of different stand and canopy structures but of the same basal area. However, the differences in growth parameters are less pronounced when the soil conditions are good than when the soil is poor.

3) Tree regeneration and early growth of forest stands can be maximized by matching growth environments and species, based on the species' light tolerance.

4) Matching tree seedling and within-gap position will maximize growth rates in CCF (CGSS).

5) Light conditions to a large extent explain differences in seedling growth between different stand treatments in CCF.

6) A radiation simulation model and biomass estimation by image analysis can be useful tools for finding effective ways of managing solar radiation regimes of forest stands and evaluating regeneration success.

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