Occurrence, Morphology and Growth of Understory Saplings in Swedish Forests

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Abstract

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Growing demands for a multipurpose forestry leads to increased use of silvicultural systems that avoid clear-cutting. Regeneration in such systems is based on establishment and ingrowth of new seedlings under a more or less closed canopy. At long-term forestry planning reliable ingrowth models are needed to predict the future wood production. The objectives of this thesis were to review the field of ingrowth in established stands, to develop a model for prediction of ingrowth for the planning system Heureka and to deepen the insight in the ingrowth process by a case study.

The ingrowth model consisted of four parts, describing:
Probability for occurrence of saplings (1-39 mm diameter at breast height (DBH)) on plots with r = 5 m.
Number of saplings on stocked plots (plots with saplings of target species).
Probability for ingrowth of a sapling over 39 mm DBH during a 5-year period.
Diameter of ingrown trees at the end of the 5-year period.

The model was based on data from permanent plots at the National Forest Inventory. Separate functions were developed for seven species and species groups. *Picea abies* saplings had the widest distribution and occurred on 58 % of 12 469 representative plots in established forests. *Betula* spp. saplings occurred on 50 % of the plots, while the occurrence of saplings of other species was less than 20 %. Sapling density on stocked plots was highest for *Betula* spp, in average 10 per plot. Average ingrowth rate was 14.6 stems per ha and year, and *P. abies* made up more than half of this. The ingrowth varied according to the different functions with age, density and species composition of the stand and the moisture and fertility of the site.

Growth and morphology of young conifers was examined in a species experiment on a clearcut and in shelterwoods of three different densities (41 – 124 stems per hectare). The largest intra-specific differences between clearcut and shelterwood were found for *Pinus* spp, while moderate differences were found for *Picea* spp. For *Pinus* spp, stem height and diameter decreased, while the stem slenderness increased with increasing shelterwood density. Moreover, the number of branches per whorl and the crown ratio decreased with increasing shelterwood density. The proportion of biomass in roots, stem, branches and needles was analysed as a function of estimated irradiance transmission for each individual. The proportion of stem decreased and the proportion of branches increased with increasing irradiance for *Pinus* spp. No significant trends were found for *Picea* spp.

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Appendix

Articles I-IV

The present thesis is based on the following articles, which will be referred to by their Roman numerals:

I. Wikberg, P-E., Elfving, B. and Kempe, G. Modelling understory sapling density and distribution in Swedish forests. Manuscript.
II Wikberg, P-E. and Elfving, B. Modelling ingrowth of saplings into the tree layer in Swedish forests. Manuscript
III Wikberg, P-E., Elfving, B., Lundmark, T. Ottosson-Löfvenius, M. and Rosvall, O. Biomass growth and allocation patterns among planted conifer saplings in varying overstory densities. Manuscript.

Introduction

Regeneration of natural forests generally takes place as establishment of seedlings and ingrowth of trees under a more or less open canopy (Kuuluvainen 1994, Linder et al. 1997). In commercial forestry regeneration is generally performed through planting after clear-cutting. For modelling of regeneration at long-term forestry planning both ways of forest regeneration must be covered.

Forestry in Sweden as in many other parts of the world is undergoing an adaptation to demands raised by groups representing non-forestry related values. Examples of such values in Sweden are nature conservation, recreational values and reindeer herding. The adaptation of forestry to non-forestry related values results in forest management systems where the traditional clear-cutting forestry is partially replaced by various kinds of partial harvesting systems, avoiding the clear cutting phase (O'Hara 1998). Thus the demand for reliable ingrowth models has increased.

The systems used as planning instruments for forest management during the last decades in Sweden are totally adapted to wood production. These systems are the Hugin system (Lundström & Söderberg 1996) and the Forest Management Planning System (FMPS) (Jonsson et al. 1993). Both systems will be replaced by the multi-purpose Heureka forest planning system, which integrates inputs from a range of fields, such as ecology, soil sciences, environmental disciplines, and traditional forestry (Lämås & Eriksson 2003). Forest development in the Heureka system will be predicted by singletree distance independent models for generation, growth and mortality.

The objectives of this thesis were to review the field of ingrowth in established stands, to develop an ingrowth model for the planning system Heureka, and by a case study deepen the insight in the development of more or less shade-tolerant species under different shading conditions.

Seedlings and saplings that are clearly separated from the overstory in size and age, and are established before cutting are termed advance growth. They form a source for regeneration both after partial harvest (e.g. Örlander & Karlsson 2000) and after clear cutting (Andersson 1988). No study has so far been published on the occurrence of advance growth in Swedish forests. Earlier investigations have mainly focused on virgin forests (e.g. Leemans 1991, Hofgaard 1993 a,b, Linder et al. 1997). Other studies have focused on the survival and development of advance growth after cutting (Örlander & Karlsson 2000, Granhus & Fjeld 2001). Thus, an investigation of the supply of advance growth in managed stands is needed.

Overview of modelling approaches

Two main modelling approaches can be distinguished for predictions for the recruitment of seedlings, saplings or trees in established stands: regeneration models and recruitment models (Vanclay 1994). Regeneration models start with some of the processes behind the seedling establishment, while recruitment models start with already established seedlings or saplings. Vanclay (1994) did not differ between the terms recruitment and ingrowth. Lundqvist (1995) used the term recruitment for the birth of a sapling and ingrowth for saplings that grew into the tree stratum. This was the terminology used in this thesis.

Pukkala (1987) developed models for natural regeneration for Norway spruce, Scots pine and birch that included birth, growth and mortality of seedlings. The birth process included submodels for seed crop, stockable area, proportion of full seeds, proportion of mature seeds, predation of seeds, germination, and number of seedlings. A stochastic approach was used where uniformly distributed random numbers were compared to frequency distributions for the different parameters to estimate the probabilities for different outcomes. He stated that data for constructing and testing the models were difficult to obtain. Beside the purpose of the model, i.e. to predict regeneration after regeneration cuttings, it provides valuable contributions to our understanding of the processes behind regeneration. The model was further developed by Pukkala & Kolström (1992), which included a spatial component for the effect from the parent tree on seed rain and growth resources. The purpose of Pukkalas model was to predict regeneration after cuttings leaving seed trees followed by soil scarification. Detailed regeneration models are needed to predict forest development after certain silvicultural treatments (Ek & Monserud 1974). In growth models for large scale and long term planning where the average outcome at different site and stand types are in focus, a recruitment model based on representative empirical data should be more efficient.

Vanclay (1994) differed between static and dynamic recruitment models. In static models, it is assumed that the amount of observed recruitment during the data collection represents the long term average. The input of new recruits will thus not vary greatly during simulations (Pacala et al. 1993, Kolström 1993). Other models predicts number of recruits as a function of site and stand data (e.g. Vanclay 1992, Ferguson & Carlson 1993, Schweiger & Sterba 1997). Vanclay (1994) argued that dynamic approaches should be used if data permits.

Events like sapling occurrence and ingrowth on a plot is afflicted with great variability. Such highly stochastic procedures can be modelled by using a two-stage approach, where the probability of an event is estimated in step one, and the magnitude of the event in step two. Such approach was for instance used by Hasenauer & Kindermann (2002) for assessing regeneration establishment and height growth in uneven-aged stands. Probability of regeneration of any species was estimated in step one, density in step two, and probability for a particular species in step three. Height growth was calculated for representative trees by species and height class, as a function of competition from overstory, regeneration and the distance from stand edges (Hasenauer & Kindermann 2002).

The Hugin system has been used in long-term planning in the last 30 years in Sweden (Lundström & Söderberg 1996). In this system, regeneration after clear-cut has been modelled through an imputation system (Elfving 1982), and models for ingrowth in established stands were also used (Hägglund 1981). The ingrowth component was constructed in a four-step approach. In step one, plots were identified where trees smaller than 5 cm DBH was present. A discriminant function was used to discriminate between stocked and non-stocked plots. A discriminant score was calculated for each of the two groups using stand and site variables as independent variables, and a mean score was calculated from the two scores. A plot was judged as stocked, i.e. target species occurred on the plot, if the score for the plot was larger than the mean score, and as non-stocked otherwise. In step two, the amount of such trees was estimated. In step three, the amount that annually passed the ingrowth limit 5 cm DBH was estimated (Hägglund 1981), and in step four the size of the ingrowth trees was estimated.

Hamilton & Brickell (1983) presented an approach where the dependent variable in step number one was dichotomous and calculated using logistic regression (Hamilton 1974). This approach was for instance used by Schweiger & Sterba (1997), Ferguson & Carlson (1993) and Vanclay (1992), and was chosen for construction of the models presented in this thesis.

The models for predictions of forest development within the Heureka system include singletree distance independent models for regeneration, mortality and growth. The growth models in the new Heureka system are based on data from the national forest inventory (NFI) permanent plots, and contain four functions: distance independent basal area growth functions for single trees, height functions for single trees, height growth functions for single trees, and volume functions for single trees. The regeneration process is divided into two parts as in the Hugin system. Regeneration after clearcutting is simulated by an imputation system, where data from measured plots in young evenaged stands is linked to plots to be simulated. Regeneration within existing stands is simulated with an ingrowth model, that specify the species, size and number of trees that are expected to pass a predefined size limit during a five-year period.

Factors affecting the occurrence and growth

Norway spruce is the most important late successional species in fennoscandia (Engelmark & Hytteborn 1999). It is capable to establish and survive under a closed canopy and sustain for a long time (Leemans 1991, Hofgaard 1993 a,b). Scots pine is considered as an early successional species but may establish under a canopy, especially on dry sites where it competes successfully (Engelmark & Hytteborn 1999, Steijlen & Zackrisson 1986). The broad-leaves are confined to early successional stages but occur in the understory, particularly within or close to gaps (Hytteborn et al. 1987, Linder et al. 1997).

The occurrence of a sapling of a certain size depends on establishment, survival and longevity within the size interval studied. Whether a seedling succeeds in establishing depends on the supply of seeds of sufficient quality, availability of suitable seedbeds and early mortality rate. The most important factor limiting the production of seeds seems to be the temperature. The production of seeds, seed weight and seed quality are in general negatively affected as the climate gets colder (Hagner 1965, Andersson 1965, Skoklefald 1966, Simak 1974). Germination rate and germinant growth are also negatively affected by low temperatures (Winsa & Sahlén 1995). Some microhabitats are more suitable for establishment than others. Seedling establishment is enhanced on disturbed spots of bare mineral soil (Kuuluvainen & Juntunen 1998, Nilsson et al. 2002). Kuuluvainen & Juntunen (1998) found 91 % of the birch seedlings and 60 % of the Scots pine seedlings in uprooted pits and mounds, in an old Scots pine dominated forest of *Vaccinium*-type in eastern Finland. The seed must have access to capillary water to germinate (Winsa 1995) and the newly emerged seedling must escape drought (Oleskog & Sahlén 1999), which is more probable in mineral soil where the water holding capacity is better than in the surrounding humus or vegetation (Oleskog et al. 2000). Another substrate with high water holding capacity is *Sphagnum* spp. mosses, which is a better substrate for seedling emergence compared to feather mosses, but may on the other hand cause higher mortality through smothering (Hörnberg et al. 1997, Ohlson & Zackrisson 1992). Decaying wood is another important substrate for seedling establishment (e.g. Simard et al. 1998). Hofgaard (1993 a) found nearly 40 % of the spruces <1,3 m on logs and stumps, which covered only 6 % of the forest floor in a pristine high altitude Norway spruce forest. Hörnberg et al. (1997) reported the same pattern in a Norway spruce swamp forest; 43% of the regeneration occurred on roots, stumps and logs that together covered 14% of the forest floor. Logs emerging from water may be the only place suitable for seedling establishment in swamps and bogs. At mesic sites, decaying wood has a higher water holding capacity than the adjacent humus layer. Logs may prolong the growing season since they are exposed earlier in spring as the snow pack melts, and the seedlings also escape competition with late successional mosses and dwarf-shrubs (Arnborg 1942, Hörnberg et al. 1997). The humus layer may be both beneficial and unbeneficial for regeneration. It constitutes a bank of nutrients, such as nitrogen, essential for successful seedling establishment and growth. At the same time, it may be an obstacle by making the nutrients inaccessible for plants as the nutrients are often bound in polyphenol complexes (Wardle et al. 1997). Hallsby (1994) showed in a greenhouse experiment that seedlings grown in a mixture of mor and mineral soil grew better than in pure mineral soil. In the field however, the humus is occupied by roots from dwarf shrubs and trees (Sirén 1955). The common dwarf shrub bilberry (*Vaccinium myrtillus* (L.)) competes successfully with seedlings of nutrients (Jäderlund et al. 1997), and its litter may have negative effect on seedling growth (Jäderlund et al. 1996). The dwarf shrub crowberry (*Empetrum hermaphroditum* (Hagerup)) has been shown to have allelopatic effects on seedling performance (Nilsson 1994, Zackrisson & Nilsson 1992, Nilsson & Zackrisson 1992) both directly by extracting phenolics compounds (Odén et al.1992, Nilsson et al. 1998) and indirectly by inhibiting microorganism activity in the humus layer (Wardle et al. 1997). Light deficiency caused by overstory density also causes mortality, especially for early successional species (Landhäusser & Lieffers 2001, Leemans 1991). Examples of other mortality or damage factors are predation from slugs (Nystrand 1998), and browsing from ungulates that may prevent seedlings and saplings from reaching tree size (Angelstam et al. 2000, Linder et al. 1997). The importance of microsites of certain qualities for establishment is lower in the south than in the north (Kuuluvainen 1994). Örlander & Karlsson (2000) found high densities of Norway spruce seedlings prior to shelterwood cutting in southern Sweden. Leemans (1991) reported high densities of Norway spruce seedlings in a virgin Norway spruce dominated forest in south-central Sweden. The density of one-year old seedlings was very high, 200000-420000 seedlings ha^{-1}, but only 1 % were alive after one year. The one-year old seedlings were randomly distributed, while the distribution became aggregated for surviving seedlings. Saplings and sub-canopy trees were strongly aggregated and connected to gaps.

Growth of understory seedlings and saplings is negatively influenced from the overstory density (e.g. Golser & Hasenauer 1997). Light is often considered as the limiting factor for the growth of seedling and saplings under a canopy (e.g. Finzi & Canham 2000), but root competition has been shown to have high impact especially on nutrient poor soils (Björkman 1946, Christy 1986, Coomes & Grubb 1998). Tree species composition in the overstory can also affect the growth of the understory. Kuusipalo (1985) showed that not only stand density was important for estimations of canopy openness; increasing proportion of Norway spruce did also decrease the canopy openness.

Factors affecting the occurrence and growth of seedlings and saplings thus form a complex network of parameters like climate, stand species composition and density, forest floor vegetation and site productivity. These factors must be considered in models aiming at predicting the occurrence and growth of saplings in established forests.

Morphological response among saplings under a canopy

Plants respond to shading from competitors by increasing the internodal elongation (Raven et al. 1992). For juvenile trees growing under a canopy, this should mean that the growth is allocated to height growth in a higher rate than if the canopy was absent. This response affects the morphology of the tree. If height growth is promoted, the allocation of biomass to the stem should be promoted at the expense of other parts of the tree. The morphological response to competition among young conifers in single layered stands is fairly well documented, which is not the case for young conifers under a canopy.

Pine tends to allocate more of its biomass to height growth as competition increases. The height - diameter ratio has been shown to be higher among pines subjected to competitive stress (Williams 1999 et al., Naidu et al. 1998, Gavrikov & Sekretenko 1996, Fries & Nilsson 1990). Naidu et al. (1998) found that suppressed loblolly pines (*Pinus taeda* (L.)) allocated more growth to stem than to branches and needles compared to dominating trees. Similar results were reported by Nilsson & Albrektson (1993). They showed that the stem wood production of suppressed Scots pine in single layered stands was of higher priority than for dominating trees.

Shade tolerant conifers, such as spruce and fir, tend to lower their height growth in favour to branch lateral growth in deep shade. Thus, the heterotrophic to autotrophic ratio is maintained at a low level. This should be advantageous under a canopy where the amount of light does not increase in proportion to tree elongation (Duchesneau et al. 2001, Messier et al. 1999, King 1997). In moderate shade, as in shelterwoods, it has been found that Norway spruce increases its height - diameter ratio compared to trees growing on clearcuts (Bergqvist 1999), and to decrease the number of branches (Klang & Ekö 1999). Nilsson & Hällgren (1993) found that artificial shading increased the allocation to stem and decreased the allocation to needles.

Most studies concerning juvenile tree morphology have been conducted in single layered stands where differences between dominating and suppressed trees have been investigated. In this thesis, an investigation is presented where the morphology of young conifers on a clearcut was compared to young conifers growing in shelterwoods.

Objectives

The objective of this thesis was to investigate the properties and dynamic of the understory sapling population in Sweden. More specifically, models for prediction of the occurrence, amount and ingrowth were made, and an investigation on conifer sapling growth and morphology in different overstory densities was conducted. Sapling occurrence, density and ingrowth were investigated through constructing models adapted to the Heureka forest planning system.

The objectives of the included papers were:
construct models for the occurrence, density and distribution of saplings in Sweden (Paper 1)
construct models for the ingrowth of trees from the sapling stratum in Sweden (Paper 2)
investigate the growth and morphological response among young conifers to different shading conditions (Paper 3).

Material and Methods

Paper I and II

A precondition for the development of an ingrowth model covering all possible conditions in Sweden was that data from the National Forest Inventory (NFI) could be used. Information on seedlings < 130 cm height was lacking in available data. Thus the study was directed on the sapling population, which was defined as trees with a diameter at breast height (DBH) of 1-39 mm. Different parts of the model were based on different data sets and presented in different papers.

The ingrowth model consisted of four parts:

1. probability functions for the occurrence of at least one sapling of target species on a certain plot (I)
2. functions for estimation of the number of saplings in plots with saplings (I)
3. probability functions for a sapling passing the ingrowth limit 40 mm DBH during a five-year period (II)
4. functions for estimation of the diameter of ingrowth trees (II)

All functions were based on data from the NFI permanent plots (Ranneby et al. 1987). The NFI is a stratified survey where circular sample plots are arranged along the sides of rectangular or squared tracts. Side length varies between 300 m to 1800 m. The tracts are systematically distributed all over Sweden, with a denser spacing in the south than in the north. Some tracts are temporary and some are permanent. The permanent tracts were established and inventoried for the first time during the period 1983-1987 and these measurements formed the bases for paper I.

The second inventory was made during 1988-1992, and the third inventory during 1993-2002. Data from inventory 2 and 3 was used for paper II. In about 18500 permanent circular plots of radius 10 m (area 314-m^2), the diameters of all trees ≥ 100 mm DBH, were measured. Site- and stand data was also collected. In inventory 1, small trees (< 100 mm DBH) were measured on a subplot with 5 m radius and the same plot centre as the 10 m plot. Of these trees, saplings of DBH < 40 mm were chosen for the analysis in paper I. In inventory 2 and 3, trees of DBH < 100 mm were measured and coordinated within the first quadrant, which was the quarter sector from north to east of the 5 m radius plot (area = $(5^2 \pi)/4 \approx 20$ m^2). Ingrowth limit was set to DBH 40 mm and thus, saplings of DBH < 40 mm measured at inventory 2 were chosen for the analysis. Sprouts from stumps were divided into the DBH classes < 20 mm and 20-39 mm by the NFI. In the lower size class there was only one shoot per stump measured. Stands belonging to cutting classes below 23 (mean height of dominating trees < 3 m) (Anon. 1983) were excluded. A further restriction was that at least one tree with DBH ≥ 100 mm had to be present within the 10 m plot. Of plots located on stand borders, only those with a 5 m subplot completely within the stand were accepted. In total, 12469 plots fulfilled all demands and were used in paper I. In paper II, 10897 plots fulfilled all demands and the total number of trees of DBH < 40 mm on these plots was 29590 at inventory 2 out of which 14647 were found and re-measured at inventory 3. Of these trees, 1647 were denoted as ingrowth. The individual measured tree was the unit of replication in the data set; the number of observations was thus 29590. The probability of a sapling passing the ingrowth limit between inventory 2 and 3 was calculated using site and stand data from the 10 m plot as explanatory variables. The time interval between inventory 2 and 3 varied from 5 to 10 years. The time interval in the ingrowth models had to be recalculated to 5 years since the growth models that will include the ingrowth models are adapted to 5-year intervals. Therefore, the diameter growth between inventory 2 and 3 for each tree was divided with number of years between measurements, multiplied by 5, and added to the diameter at inventory 2. Ingrowth was denoted by 1 if the resulting DBH was ≥ 40 mm, and 0 if DBH was < 40 mm.

Separate models for sapling occurrence, density, ingrowth and diameter of ingrowth trees were made for seven species and species groups (Table 1).

In paper I, models for the probability of sapling occurrence were made using site and stand data from the 10 m plot as explanatory variables. Logistic regressions were used for the estimations. Then, models were made for the sapling density in plots where the target species occurred, using the dependent variable from the logistic regressions and some site and stand variables as explanatory variables in non-linear regressions.

In paper II, models for the proportion of ingrowths were made by estimating the probability of ingrowth for saplings using logistic regression. Models for the diameter of ingrowths were made using linear regression.

Table 1. *Species and species groups for which models for probability of occurrence, density, and ingrowth were made*

Species or species group	Species included	
	Common name	Scientific name
Scots pine		*Pinus sylvestris* (L.)
Norway spruce		*Picea abies* (L.) Karst.
Birch	downy birch	*Betula pubescens* (Ehrh.)
	silver birch	*Betula pendula* (Roth.)
Other boreal broad-leaves	rowan	*Sorbus aucuparia* (L.)
	aspen	*Populus tremula* (L.)
	goat willow	*Salix caprea* (L.)
	alder	*Alnus glutinosa* (L.)
	grey alder	*Alnus incana* (L.)
	Norway maple	*Acer platanoides* (L.)
	sycamore	*Acer pseudoplatanus* (L.)
Oak	pedunculate oak	*Quercus robur* (L.)
	sessile oak	*Quercus petraea* (Matt.) Liebl.
Beech		*Fagus sylvatica* (L.)
Other hemiboreal broad-leaves	small-leaved lime	*Tilia cordata* (Mill.)
	large-leaved lime	*Tilia platyphyllos* (Scop.)
	ash	*Fraxinus excelsior* (L.)
	Wych elm	*Ulmus glabra* (Huds.))
	small-leaved elm	*Ulmus minor* (Mill.)

At application, the number of ingrowths each five-year step is calculated by applying the estimated probabilities for ingrowth per tree from paper II on the estimated sapling densities from paper I, as the proportion of ingrowth. The density modelled from inventory 1 was preferred since the plot size was the same as the plot size used for trees of DBH 40-100 mm in the growth models to which the models presented in this thesis were adapted. A uniformly distributed random number between 0 and 1 decide whether sapling occurs in the plot or not. If the random number is lower than the estimated probability of occurrence, the plot is judged as stocked, and the number of saplings is estimated. The estimated probability of ingrowth is applied on the number of saplings per plot as the proportion of ingrowth trees, and thereby as the number of ingrowths. Thereafter, the diameter of ingrowths is estimated and the ingrowth trees are incorporated in the growth models of the Heureka planning system (Elfving 2001).

Paper III

Data for paper III was collected in a shelterwood trial at Åheden at the Vindeln Experimental Forest (Anon. 1985) in Vindeln, northern Sweden (64° 14’N, 19° 49’E, 175 m.a.s.l.). The trial was located on a flat sandy silty sediment soil. The forest floor vegetation was dominated by *Cladina* spp. lichens, the feather moss *Pleurozium schreberi*, heather (*Calluna vulgaris* (L.)), and lingon berry (*Vaccinium vitis-idaea* (L.)). The trial was established in 1982 in a stand of about 20 m high and 170 years old Scots pine. The stand was harvested during the winter 1983-84, leaving one clearcut and three shelterwoods of about one hectare each, surrounded by undisturbed forest. Shelterwood densities were 48, 91 and 138 stems per hectare. Mounding followed by planting was done in plots of about 40 * 80 m on the clearcut and in the shelterwoods in 1988 and 1989. Two plots were established on the clearcut and one plot was established in each shelterwood, i.e. totally five plots. Each plot was divided into two subplots. One subplot was planted in 1988 and the other in 1989. Planting with about 2.2 m spacing was done in 36 rows per subplot with 8 seedlings in each row, i.e. totally 2880 seedlings. Eight coniferous species of two or three proveniences per species, which made a total of 18 provenances, was planted. Each provenance was planted in two randomly chosen rows per subplot. The plots were fenced and the shelter tree density within the fences was 40, 106 and 126 stems per hectare in summer 2002. Summer frosts are very common in the area. The trial was originally established to investigate the effect from shelterwood on frost damages on planted conifer seedlings.

Measurements of all seedlings were made at the end of the growing season in 2002, i.e. 14 and 15 years after planting. Total height, height to lowest living branch, stem diameter at 10 cm height, diameter of thickest branch was measured, and number of branches within the whorl with the thickest branch was counted. Status was classified as; dead, severely damaged, slightly damaged or undamaged. Total biomass and biomass allocation analysis was conducted on a sub-sample of totally 85 saplings of lodgepole pine, Norway spruce, black spruce and Scots pine. The saplings were divided into root, stem, twig and needle fractions.

The species where treated separately in the analysis. Differences between plots in the parameters measured on all saplings were analysed using General Linear Model (GLM) technique. Biomass allocation to the different tree fractions was analysed using linear regression. Proportion of total dry mass for each fraction was dependent variable and proportion of estimated irradiance for each sapling independent variable. Models for biomass estimations for all saplings were made using total biomass of the sub sample chosen for the biomass allocation study. The logarithm for total biomass was used as dependent variable and the logarithm for stem diameter as independent variable.

Results and Discussion

Observed sapling occurrence, density and ingrowth

NFI-data is an ideal base for construction of large-scale empirical models. The permanent plots provide a representative cover of a wide variation of conditions, where the re-measurements make it possible to follow the stand dynamic. An advantage of using an empirical modeling approach is that the predictions made by the model usually agree well with reality. But if reality changes, the model may not be able to capture the effect of those changes. As in this case, the models were based on data from forests managed mainly with traditional even-aged system, but one of the objectives was to develop models for ingrowth applicable on forests treated with non-clear cutting forestry. Thus, the models must be tested on data from stands managed with non-clear cutting forestry to evaluate the suitability of implementing the models in these kinds of forests. Average occurrence, density and ingrowth for target species are compiled in Table 2. The average number of ingrowths was calculated by applying the proportion of ingrowths on the density from inventory 1.

Norway spruce saplings had the widest distribution and occurred on 58 % of the 12 469 representative plots in established forests (Table 2). Birch saplings occurred on 50 % of the plots, while the occurrence of saplings of other species was less than 20 %. Sapling density on stocked plots was highest for birch, in average 10 per plot. Average in-growth rate was 14.6 stems per ha and year, of which about 50 % was Norway spruce.

Table 2. *Proportion of r=5 m plots with occurrence (%), and density in plots with occurrence of target species (n/plot) at inventory 1. Proportion (%) of saplings measured at inventory 2 denoted as missing and as ingrowth (DBH > 40 mm) at inventory 3, and average number of ingrowths per hectare and year*

Species	Occurrence %	Density n	Missing %	ingrowth %	no. ingrowth $yr^{-1}ha^{-1}$
Pinus sylvestris	18	4.2	48	10	1.9
Picea abies	58	4.8	40	11	7.8
Betula spp.	50	10	53	2.4	3.1
Other boreal broadleaves	16	7.4	68	4.5	1.4
Quercus spp.	6.8	4.2	57	4.1	0.3
Fagus sylvatica	1.5	4	52	5.9	<0.1
Other hemi-boreal broadleaves	1.1	7.8	54	4.4	<0.1

Models for sapling occurrence, density and ingrowth

An overview with the main results for the most important species is compiled in Table 3.

Table 3. *Overview of the main results from the occurrence models (o), density models (d), and ingrowth models (i), + = positive correlation, - = negative correlation, +- = positive correlation that turned negative. Dots are denoting insignificant correlation. The logit-value is the dependent variable from the occurrence models*

Source of variation	*Pinus sylvestris*			*Picea abies*			*Betula* spp.		
	o	d	i	o	d	i	o	d	i
Basal area	-	+	-	+-	+	-	-	.	-
Stand age	-	.	-	-	-	-	-	-	.
Large pine occurrence (DBH>100 mm)	+	.	.	.	.	.	.	.	.
Large spruce occurrence	-	.	.	+	.	.	.	.	.
Large birch occurrence	.	.	.	+	.	.	+	.	.
Spruce proportion	.	.	-	.	.	.	.	.	.
Spruce sapling occurrence	+	.	.	.	.	.	+	.	.
High site fertility	-	.	+	+	.	+	.	.	+
Low site fertility	+	.	.	-	.	.	-	.	.
Temperature- sum	-	+-	.	+-	+-	.	.	.	.
Altitude	-	.	+	.	.	-	.	.	.
Latitude	.	.	.	.	.	.	-+	.	.
Soil moisture	-	.	.	+	.	.	+	.	+-
Performed thinning	-	.	.	-	.	+	-	.	.
Peat	.	.	.	.	.	.	+	.	.
Logit-value	.	+	.	.	+	.	.	+	.

The occurrence of a larger tree of target species within the 10 m plot was the overall strongest variable for prediction of probability of occurrence. It indicated suitable site conditions of target species. The negative influence from the occurrence of a large Norway spruce on the occurrence of Scots pine saplings, and the negative correlation between Norway spruce proportion and Scots pine ingrowth might be due to the higher light interception of Norway spruce compared to Scots pine and broad-leaves at a given basal area (Kuusipalo 1985).

Stand density, expressed as basal area measured at the 10 m plot, was highly significant in the probability of occurrence models for most species except for Norway spruce. This is in line with the species niche in forest succession, where Norway spruce is the most important late successional species in Fennoscandia. The occurrence of Scots pine was enhanced at nutrient poor sites, while the other species were not, which was expected since Scots pine is known to compete successfully at poor sites. (Engelmark & Hytteborn 1999). There should be some co-variation between the occurrences of different species, which was not taken into account in the modelling approach chosen since separate models were made for different species or species groups. Occurrence of a Norway spruce sapling (DBH < 40 mm) was therefore included as an independent variable in the occurrence models for the other species as an indicator of suitable conditions for sapling occurrence in general. It turned out to be positively correlated with Scots pine and birch occurrence. The decline in occurrence with increasing stand age can be explained by ingrowth, mortality, and lack of new recruitment into the sapling stratum. The ability of Norway spruce to establish and maintain under a closed canopy is well known (e.g. Leemans 1991, Hofgaard 1993 a, b, Niklasson 2002). Ingrowth of Norway spruce was negatively correlated with basal area, which further confirms its ability to grow slowly and sustain under a canopy. However, the occurrence of the early successional birch species was of the same magnitude as for Norway spruce over stand age. The combined effect from stand age and stand density suggests that birch was able to maintain over the stand rotation period but was restricted to gaps, causing a scattered spatial pattern (Hytteborn et al. 1987, Leemans 1991). The logit value was the dependent variable in the occurrence models, and was used as independent variable in the density models. Birch occurrence decreased with increasing stand age, which means that the density also decreased. However, stand age was also included in the birch density model, which means that the decrease in density over stand age was more rapid than the decrease in occurrence.

Species differed in their response to geographical and climate variables. Altitude was included in the ingrowth models for Norway spruce (negative) and Scots pine (positive). Ingrowth of both species increased with site index. However, the decrease in site index was not enough to explain the decrease in ingrowth with increasing altitude. This was adjusted by the inclusion of altitude in the models.

The attempts of constructing ingrowth functions for all broadleaves except birch failed. The mean values of ingrowth trees during 5 years should be used instead. The residuals over included variables indicated well-adapted partial relations. The occurrence and density models were validated on a data set from the Hugin young stand survey (Elfving 1982). The test material consisted of 14 naturally regenerated and 13 planted stands of Scots pine at a mean stand age of 45 years in central and northern Sweden. The validation showed fair agreements in general. However, the number of Scots pine was moderately overestimated, and the proportion of plots with birch was strongly underestimated. Such deviations could not be detected in stands from the NFI-data with about the same characteristics as in the test material. The deviations observed in the test for Scots pine and birch were probably as one could expect in a data set of wide geographical distribution and relatively low number of observations.

The logit value was shown to be a good predictor of the density, but the residuals indicated that some variables included in the occurrence models should be included in the density models as well. For instance, basal area was strongly negatively correlated with Scots pine occurrence. Basal area was also included in the density model, where it was positively correlated with Scots pine density in plots where Scots pine occurred. Thus, the Scots pine density was higher in a dense stand than in a sparse stand given the same probability of occurrence. The models for beech and other hemiboreal broad-leaves showed larger residual deviations than those for the other species or species groups, probably mostly due to the low number of observations.

Advance growth is defined as seedlings and saplings established before harvest, clearly differed from the overstory both in age and size. Thus, in a forestry context, seedlings and saplings in forests are usually denoted as advance growth. Seedlings with h<1.3 m were not measured by the NFI at the measurements used in this study. To provide information of the amount of advance growth, this stratum should have been included. However, the occurrence of saplings according to our definition should indicate the capacity of the site and stand type to carry advance growth.

The ingrowth models were adapted to growth models constructed for five-year predictions. It remains to be studied how the sapling population within the plot will be composed at each 5-year interval. A plot that is judged as stocked by the random number procedure might be judged as not stocked at the next 5-year step although the estimated probability of sapling occurrence (p) is the same at both occasions. The estimated sapling density from the first time step will then disappear at the next time step. This is unrealistic, since saplings that do not grow in to the tree strata will to a large extent be present at the next time step. A possible solution is to draw random numbers only for plots where the estimated p changes. If p increases, a random number is drawn for non-stocked plots. If the random number turns out to be within the interval between p from previous time step and the present, the plot will change from non-stocked to stocked. If p decreases, a random number is drawn for stocked plots. If the random number turns out to be within the interval between the p values from previous time step and the present, the plot will change from stocked to non-stocked.

Morphology of understory saplings

Scots pine and lodge pole pine showed a far greater morphological response to the understory environment than the other species. Stem slenderness (height / diameter ratio) was significantly higher and number of twigs significantly lower in the shelterwoods than on the clearcut. The increase in stem slenderness and decreasing number of twigs among Scots pine and lodge pole pine agrees with results from other studies (Fries & Nilsson 1990, Gavrikov & Sekretenko 1996, Williams et al. 1999). The biomass allocation study showed a negative correlation between stem proportion and estimated irradiance, and a positive correlation between twig proportion and irradiance, which agrees with studies of pine under competitive stress in single layered stands. Naidu et al. (1998) reported that suppressed loblolly pine (Pinus taeda (L.)) had a higher stem proportion and a lower proportion of needles and branches than dominating trees. Similar results were shown by Nilsson & Albrektson (1993) on Scots pine. The pine species in this study invested more resources in height growth if shaded.

The spruce species were little affected by the shelterwoods. The best growth was found in plot 1 (clear cut) and 4 (intermediate shelterwood). This disagrees with the results in the ingrowth model where Norway spruce ingrowth was negatively correlated with stand density. The growth was probably limited by something else than the shelter trees. The site was rather dry and nutrient poor, unsuitable for Norway spurce. The shelterwoods were probably not dense enough to induce any clear changes in morphology among the spruce species.

The morphological response is probably not induced by the lower amount of irradiance. The shelter trees absorb the red light, which means that the red: far red light ratio is lower under the shelter trees than above. Plants react to depletion in the red: far red light ratio by increasing the stem elongation (Raven et al. 1992). Thus, the increased allocation to height growth among the pine species was probably a response to this change in light quality. The depletion in red: far red light ratio caused by the shelter trees was probably “interpreted” as shading from competitors by the saplings. The increased allocation to height growth was likely a way to avoid overtopping by competitors.

The morphological response among the pines in the shelterwoods indicates that several characteristics that are considered as positive for wood quality can be developed when grown in shade, such as low radial growth and low stem taper.

Concluding remarks

The results presented in this thesis provide new knowledge about the development of the understory in Swedish forests. The models presented were constructed to predict the ingrowth over five-year intervals into the tree stratum in the Heureka-system. The whole growth model system was constructed to predict forest development irrespective of what management system used. The NFI-data that was used to construct the models did however not cover the whole range of thinkable management system. The models must therefore be tested on data from forests that have been treated with different kinds of partial harvest methods. The models presented here provide rather coarse predictions that should be good enough to fulfil the purpose of the models. However, if the usage of partial cutting system will increase, much more detailed investigations must be conducted to provide adequate knowledge on how to manage the regeneration in such forests and how to model its development. The effects from specific treatments on the regeneration cannot be predicted with the models presented here, due to the delay between treatment and occurrence of saplings. Thus, specific studies of advance growth must be performed to further improve the tools for modelling of ingrowth.

The height growth should be a more efficient variable for the growth than a diameter threshold value as used in the ingrowth models, to capture small changes in growth response after treatments. If the advance growth stratum is not abundant enough, other regeneration methods must be considered. One alternative is planting with or without preceding soil scarification. One advantage with planting is the possibility to choose species. As shown in the sapling occurrence models, Norway spruce is the most common species, but it might not be the most suitable or desired species. Scots pine or lodge pole pine could be an alternative if the post-harvest stand is sparse enough for the shade intolerant pine. As shown in this thesis, the pine species can grow rather well in shelterwood conditions, and develop positive features from a timber quality perspective. Studies on the different species demands of growth resources must be conducted to provide instructions about the choice of species. The density and the vertical and horizontal structure of the pre-harvest stand must be expressed in an adequate way. Stand basal area that was used in the models is a good measure for average stand density, but may not be good enough for expressing the stand density affecting the growth on the individual seedling level. Instead, a measure on the gapsize or distance to surrounding trees should be developed. This is important when predicting the seedling or sapling growth, and to decide whether planting should be done in a certain spot or not. If the pre-harvest stand is dense enough to fully utilize the growth resources, no planting should be done.

Almost all of these parameters have been subject to earlier investigations. However, a broader investigation of the mentioned parameters must be done that includes data from a wide range of site and stand types, and of different treatments. Such data would enable the development of models for the prediction of a variety of parameters concerning the recruitment of trees after harvest.

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