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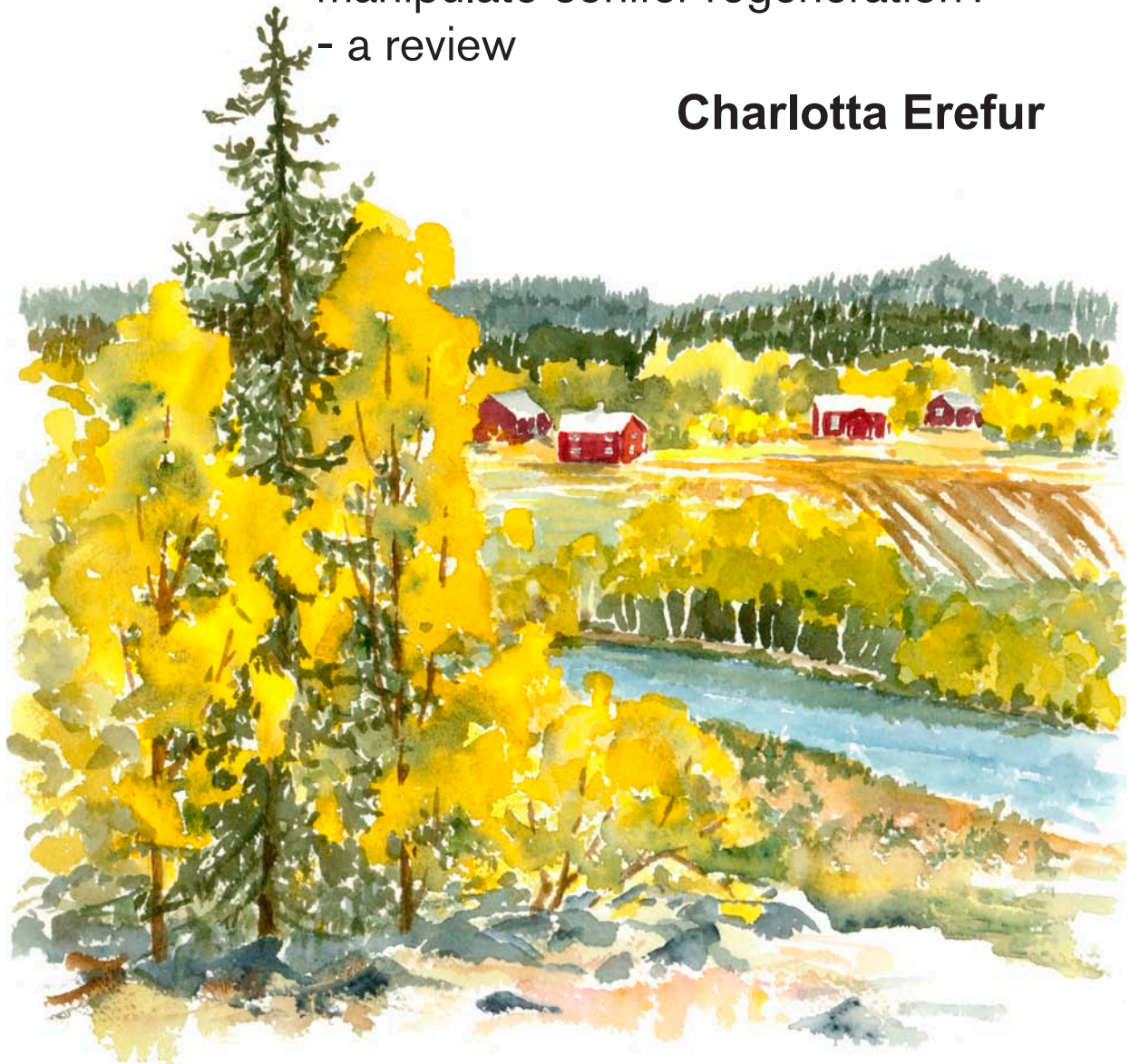
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What does forest dynamics and plant interactions tell us about the best way to manipulate conifer regeneration?

- a review

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Background

The structure of a forest has a direct bearing on energy, hydrologic and nutrient cycles within a forest ecosystem. An alteration of stand structure will influence the functioning of the ecosystem and there will be a direct effect on site microclimate, water balance and soil fertility and therefore a direct influence on the physiological response of seedlings (Grossnickle 2000).

The conifers of the boreal forest are no exceptions of being influenced by many different factors during establishment and growth, as well as germination and plant formation. Specific conditions will differ depending on the environment and plant material. Forest density together with location of the seedling compared to surrounding shelter trees, create different light, water and nutritional status. Depending on growing site, mechanical disturbances, like rain/snow and predation, will also affect the seedlings differently. It is necessary though, to try to fully understand the complex picture of competition among the seedlings.

The objectives of this paper are to review previous studies made on the following aspects of regeneration of conifers: (i) nutritional status, (ii) light availability, and (iii) regeneration pattern. The main concern is to get a picture of how the plants are affected by different kinds of competition within the reforestation site.

This paper is the first in a PhD project called "Regeneration under shelterwood - control of some environmental factors." The overall aim is to characterize different plants depending on source and growing environment and try to understand how the environment can be moderated in combination with the plant material to get a cost-effective regeneration of forest under shelterwood.

Competition within the reforestation site

Natural conditions provide environmental heterogeneity both in space and time. There is daily as well as annual variation. The effect of variation at these different scales depends on

the plants rate of response to physiological and ecological processes of interest. Each seedling experiences the fluctuations, and individual acclimation may be an important component of response and performance through time. Additionally, species also differ in their rate of response to environmental changes and the phenotypic plasticity of an individual has strong influence on how the scale of environmental fluctuations influences whole plant performance, i.e., growth, survival and reproductive output (Ackerly 1997). For example in forest gaps, individuals located on the west side receive much light in the morning hours when CO₂ levels are high and tissue water potential is less negative. The plant 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 CO₂ levels are no longer high and plant tissue water potential has become more negative. In the latter case, 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 and Grace 1997).

Nutrient availability and allocation

Changes in allocation

It is almost always noted that a change in availability of nutrients will affect the growth of a tree. For instance Malcom and Ibrahim (1993), show that the growth rate and the nitrogen uptake are strongly related. The bond is not direct though, and the allocation will control the growth of different parts of the plant (Axelsson and Axelsson 1986). Thus, a change in availability of nutrients (or of their absorption) will first of all modify the allocation of the nutritive substrates concerned, involving a growth modification of certain parts of the plant and sometimes of the whole tree. The allocation is thus the central phenomenon between the absorption and the growth of plants. In addition to the modification of allocation, a change in availability of nutrients involves the phenomenon of translocation, which is characterized by a flow of nutrients between different parts of the plant. Translocation enables a quick reaction of the plant to changes in nutrient availability, but is also a current phenomenon between for example ephemeral and perennial tissue (King, Albaugh et al. 1999) or between the old and the

new tissues (Proe, Midwood et al. 2000). We can thus conclude that a change in allocation is due to a variation in availability of nutrients, but it is also controlled by the ontogenetic development of the tree such as the senescence of the foliage. A comparative study between the genders *Picea*, *Pinus* and *Pseudotsuga* by George et al. (1997), shows significant response of these genders to the availability of nutrients in the soil. Burgess (1990) and Griffin et al. (1995) can demonstrate different reactions between species from the same gender to the availability of carbon and nitrogen. Lascoux and Lundkvist (1992) present a study showing that the responses of different settlements of *Pinus sylvestris* (L.) to various nutritive treatments are identical. In addition, we can notice that the stage of development and the age of the tree or the plant strongly affect the allocation.

Evaluation of allocation

It is possible to evaluate the allocation effect using the root/shoot ratio and the relative growth rate. Axelsson and Axelsson (1986) conclude their article by writing that the optimal root/shoot ratio, and thus the optimal biomass partitioning, could be a major determinant of growth rate capacity. According to Griffin et al. (1995), below a minimum concentration of nitrogen in the needles the growth will fade, which shows that the allocation of certain elements to certain parts of the tree can be determinant for the growth. The allocation flexibility is thus also a determinant factor in this case. That is what Grassi and Minotta (2000) say by suggesting that after a thinning, the capacity of regeneration will depend on the ability of the young seedlings to allocate more nutrients to the roots in order to maintain an adequate water supply to meet the increased transpiration demand. We also saw that the translocation plays an important part in the acclimatization of plants to a new environment.

Features like the activity of mycorrhizas (Jentschke, Godbold et al. 2001), the competition with the neighborhood of the tree (Malcom and Ibrahim 1993), the soil temperature which controls nitrogen mineralization (Domisch, Finér et al. 2000) or fertilization and irrigation treatments applied (Albough, Allen et al. 1998; Ingerslev and Hallbäck 1999) are of big

importance for allocation patterns and should not be forgotten in this context.

Fertilization

Axelsson and Axelsson (1986) show that an optimal fertilization makes an increase of allocation to the stem possible, and thus higher production of wood, for 12-year-old *Picea abies* (L.) Karst. and *Pinus sylvestris* (L.) seedlings. Burgess (1990) proposes a fertilization that increases the allocation to the roots of young spruce seedlings in nursery programs, and thus increases their root development, in order to support their adaptation to poor soil. Grassi & Minotta (2000) study the shade-sun acclimatizing of young seedlings and conclude that nutrient shortage subsequent to opening up a canopy gap, may strongly limit the acclimatizing response of Norway spruce seedlings.

Fluctuating light environments and allocation

Transient sun patches in the understory 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 patch because various physiological processes, like photosynthesis, stomatal opening, and enzyme activity, respond at different rates to the change in environment (Ackerly 1997). 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 and Bazzaz 1993). Important components of plant response to closure in forests and gap creation, are physiological and allocational responses to fluctuating light environments on longer time scales (Ackerly 1997).

De Chantal et al. (2003) showed in their study on early response of *Pinus sylvestris* and *Picea abies* to an experimental canopy gap, that pine has evolved a mechanism which allows it to increase its needle length with increasing radiation. *P. sylvestris* allocated proportionally more aboveground dry biomass to assimilating parts versus structural parts compared to *P. abies*. This made it possible for *P. sylvestris* to compete better for resources in gap and gap-edge environments.

Partial forest canopy retention systems

The forest has during the latter part of the 20th century mainly been harvested by creating clear-cuts. This method has the advantage of being rational, but it has rightfully been questioned. The following regeneration is not always successful as the local climate changes along with species distribution and nutrient/water content in the soil. At least in small-scale forestry, other methods are of interest.

A shift in *energy balance* occurs when there is a removal of the forest canopy. A much higher amount of radiant energy will reach the soil surface. This change in energy distribution clearly alters the temperatures of soil and air as well as the evaporative requirement near the ground. A mature forest stand has a rather high transpiration rate and that gives reduced and regulated stream flow through the ecosystem. The energy balance also influences snow conditions.

The *hydrological cycle* is dramatically altered in a clear-cut, which is characterized by low stand transpiration, increased stream flow, and

potentially high amount of available soil water. 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 biomass or the organic matter on the ground. The removal of biomass through harvesting reduces the nutrient content of the site and the remains come fore most from the forest floor and are rapidly being cycled through decomposition and mineralization.

The climate of the forest is overall very complex. What can be said, is that big openings are exposed to 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 directly or indirectly affect seedlings and trees, as well as forest stands, to a very large extent. The chances for survival and growth of an individual depend on the local climatic conditions. Figure 1 illustrates how great the differences in microclimate can be on a clear day at the edge of a forest in the Netherlands.

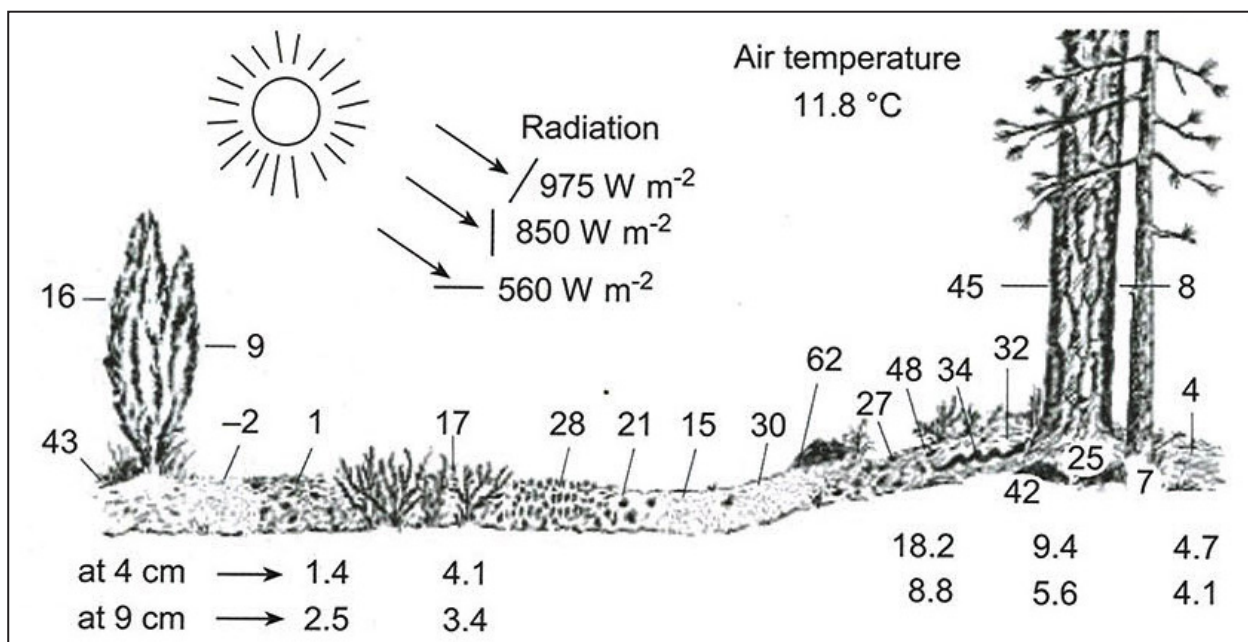


Figure 1. Surface temperatures, soil temperatures at 4 and 9cm depth, and air temperature 1m above the ground, along a transect in the Netherlands. Measurements were made at noon on a clear day in March. (Stoudtjesdijk and Barkman 1992)

Shelterwood cutting

In areas that are difficult to regenerate, as for example wetlands, areas with high risk of frost or stands where competition from surrounding vegetation is though, the use of shelterwoods when regenerating can be of advantage. The shelter trees do not only provide seeds for natural regeneration, but they also create a favorable environment for the seedlings. The ground temperature in a day is more stable in a shelterwood, than on a clear-cut, since the overstory trees to some extent prevent the long-wave radiation from leaving to the atmosphere. This will give less frequent summer frosts and frost heaving but also less incoming radiation (Hannerz and Gemmel 1994; Örlander and Langvall 1997; Örlander and Karlsson 2000). Other effects of the shelter trees, are less wind exposure, more stable soil water content (on a clear-cut there can easily be an access of water when the mature stand is removed, but also droughts as a result of extremer temperatures), and less vegetational competition for the seedlings as well as sometimes altered risk for predation from herbivores (Holgén 1999).

Shelterwood cutting is used in even-aged forests (where the trees are very close in age) and relies on natural regeneration to re-establish the stand. Initially, some of the mature trees are harvested. Those that remain provide the protection and shade needed by young trees and seedlings. The rest of the mature stand is harvested once regeneration is well established. Selection cutting is used to maintain uneven-aged stands (where the trees are of all different ages). The forest regenerates naturally, with the young trees and seedlings benefiting from the protection of existing trees.

Gap creation

Definition

How to define a gap and the importance of forest gaps have been discussed with many different aspects. How close does a seedling need to be the nearest sheltertree in order to be affected (and how is it affected)? A disturbance is considered a specific event that alters ecosystem pattern and process by disrupting community structure or changing resource availability and allocation. An essential component in defining

a forest gap is the minimum opening size to be called a gap. The ideal would be that one could define this functionally, that is in terms of forest dynamics, but that is difficult. In practice, the minimum size must be large enough for the smallest gap to be distinguishable in the complexity of forest structure (Brokaw 1982). A natural gap is formed by the death or fall of large branches, an individual tree, or a group of trees resulting in a canopy opening, usually quantified in terms of projected land area. 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 (Coates and Burton 1997).

Environmental conditions

Habitat conditions vary among gaps, within gaps, at the gap edge, and within the forest stand matrix. The gap edge and stand matrix have received little study in terms of assessing their suitability for tree establishment and growth (Coates and Burton 1997). 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 so sharply over short distances within gaps, position within gap is critically important to the physiology and growth of any individual tree seedling (Wayne and Bazzaz 1993).

Coates (2000) performed a study on the five conifer species western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), subalpine fir (*Abies lasiocarpa*), hybrid spruce, and lodgepole pine (*Pinus contorta*). The study showed that growth of all species greatly increased from small single-tree gaps to about 1000m² gaps, but thereafter little change in growth could be seen up to gaps of 5000m². In large and medium gaps (301-1000m²), the largest trees of all species were found in the middle gap position and there was for most species little difference in growth between the north and south positions. In the smaller gaps, as well as in the forest understory, total size and growth rates were almost identical for all species.

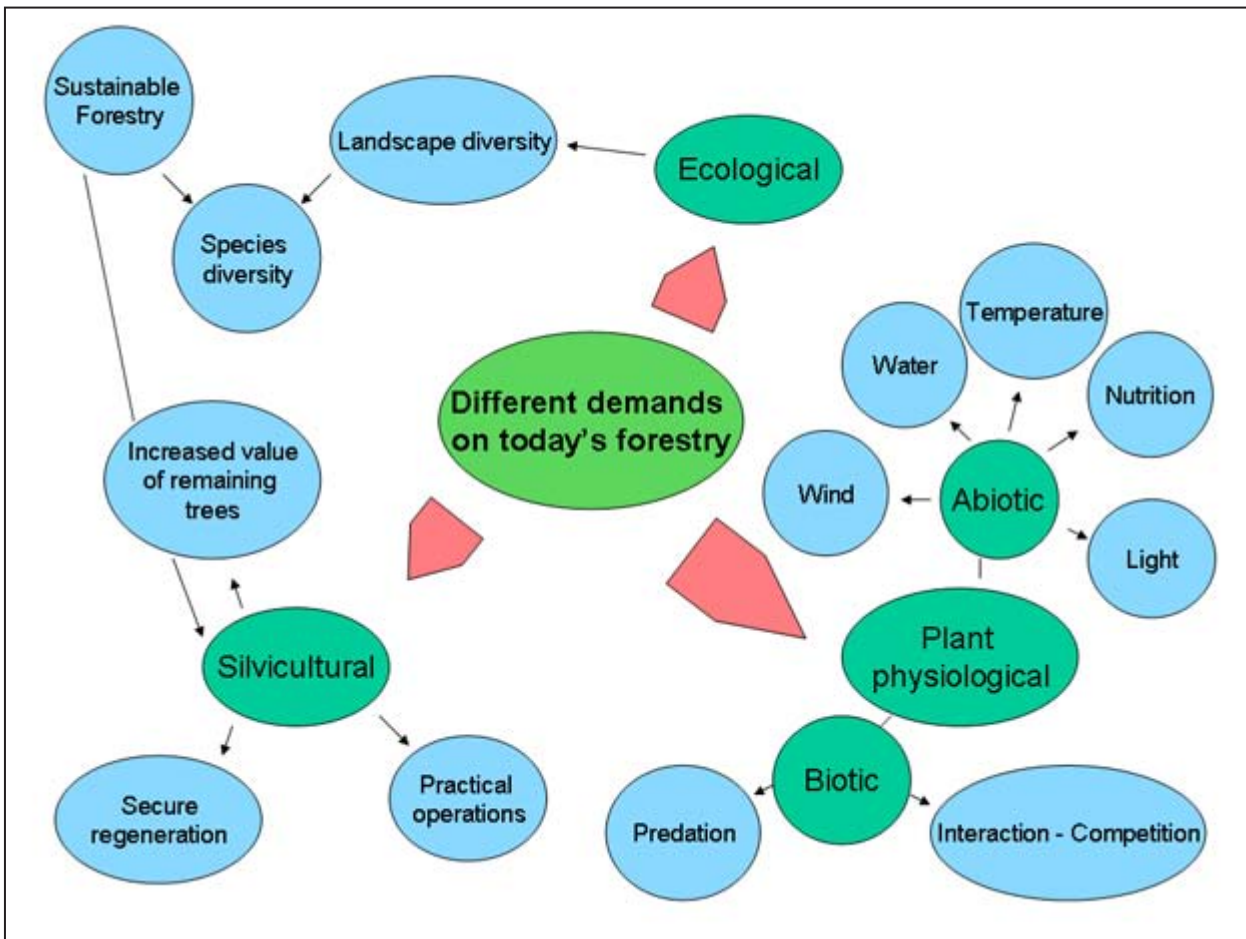


Figure 2. Schematic view of the different demands on today's forestry

The results from Gray and Spies (1996) also indicate that the seedling sizes of *Abies amabilis*, *Pseudotsuga menziesii*, and *Tsuga heterophylla* increase with gap size and are greatest at the gap centers. Further they conclude that differences in establishment among gaps were greater on natural substrates than on mineral soil. Anyway, the greatest establishment for all species occurred in the same locations on natural and disturbed microsites, and that is the moist, shaded environments in 0.2 ha gaps and the southern parts of larger gaps. Coates (2002) showed that in a mixed conifer and deciduous forest in British Columbia, Canada, seedling recruitment was abundant within canopy gaps across a wide range of gap sizes (20-5000m²), but recruitment numbers dropped rapidly under the closed forest canopy as well as in the open conditions of clear-cuts.

Careful matching of tree species to gap size and gap position can minimize early mortality and maximize growth rates. Opening sizes need not

to be very large (0.1 – 0.2ha minimum) in order for species to achieve growth rates similar to those found in the open conditions of a clear-cut (Coates 2000). The effect on biodiversity in these kinds of regeneration systems will be minimized.

Discussion and conclusions for the future

The establishment, growth, and development of trees all interact strongly with the physical environment. Better understanding of these interactions is necessary to improve our capability to predict how the productivity and development of forest ecosystems will respond to natural disturbance, climate change, and forest management. Prediction of the effect of a silvicultural manipulation must be based on the spatial as well as temporal dynamics of forest response to different kinds, sizes, frequencies, and intensities of disturbance (Coates and Burton 1997). Successful strategies

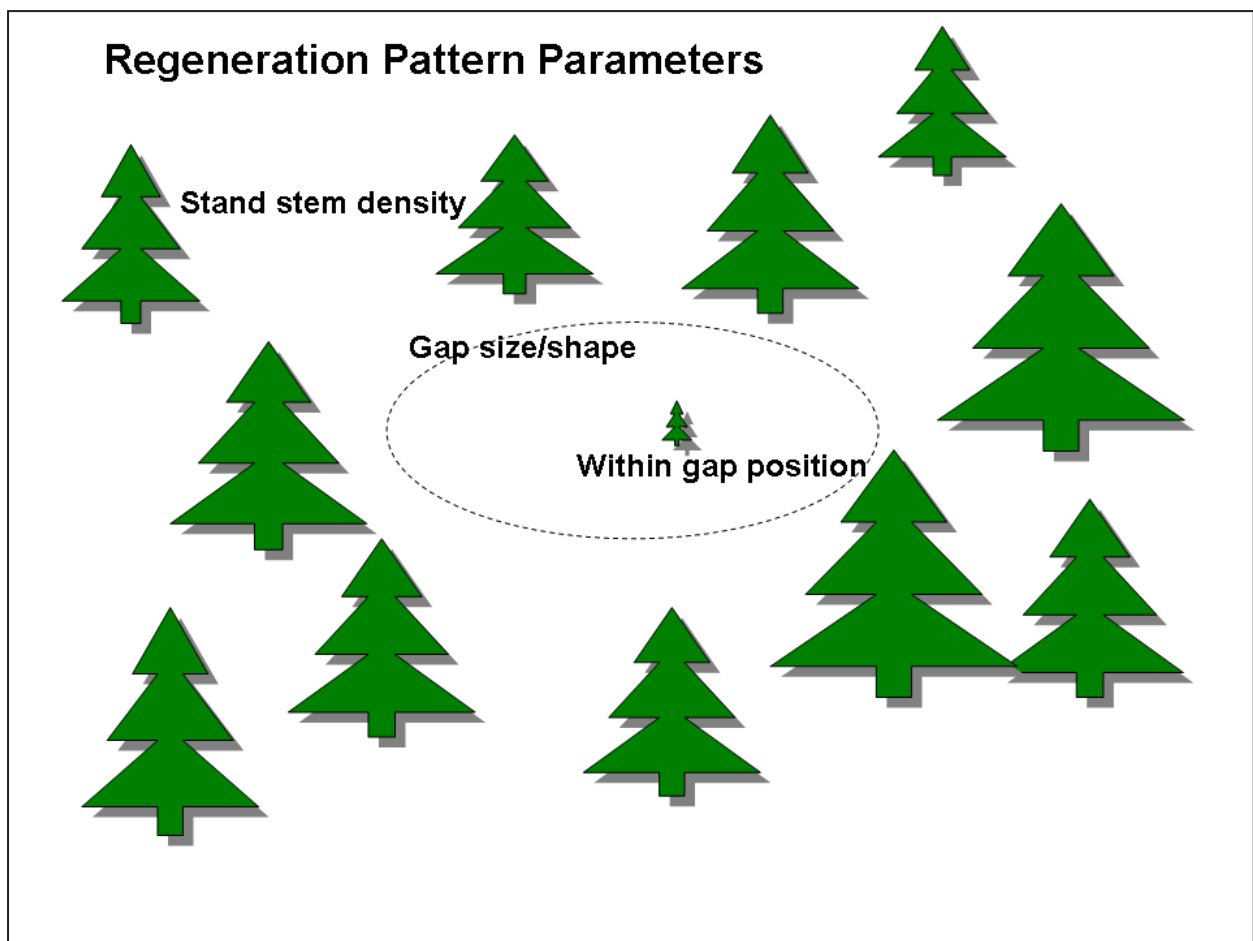


Figure 3. Parameters to consider when choosing regeneration pattern with seedling position for optimum light and moist conditions

must be based on an understanding of interactions among shelter, vegetation, the physical environment, and pine and spruce response.

Silviculture and resource management options are needed to meet the challenges of a changing forest resource. The different demands on today's forestry are presented in figure 2. Forests cannot be sustained without successful renewal of one generation of trees by another. Understanding renewal and regeneration patterns and processes is critical to sustainable resource management and a keystone of future silviculture and resource management research.

A way to regenerate forests by using the benefits of shelter trees and at the same time create the desirable conditions of a clear-cut, could be a system where you form forest gaps under shelterwood. The optimum light and moist conditions for the species of concern can be met by deciding shelterwood density and gap size/within gap position (figure 3). It would give a more secure regeneration and not necessarily a slower one.

References

- Ackerly, D. (1997). Allocation in fluctuating light environments. Plant Resource Allocation. F. A. Bazzaz and J. Grace. San Diego, California, USA, Academic Press.
- Albough, T. J., H. L. Allen, et al. (1998). "Leaf area and above- and belowground growth responses of loblolly pine to nutrient and water additions." *Forest Science* 44: 317-328.
- Axelsson, E. and B. Axelsson (1986). "Changes in carbon allocation patterns in spruce and pine trees following irrigation and fertilization." *Tree Physiology* 2: 189-204.
- Bazzaz, F. A. and J. Grace (1997). Plant resource allocation. San Diego, California, USA, Academic Press.
- Brokaw, N. V. L. (1982). "The Definition of Treefall Gap and Its Effect on Measures of Forest Dynamics." *Biotropica* 14(2): 158-160.
- Burgess, D. (1990). "White and black spruce seedling development using the concept of Relative Addition Rate." *Scandinavian Journal of Forest Research* 5: 471-480.
- Coates, K. D. (2000). "Conifer seedling response to northern temperate forest gaps." *Forest Ecology and Management* 127(1-3): 249-269.
- Coates, K. D. (2002). "Tree recruitment in gaps of various sizes, clearcuts and undisturbed mixed forest of interior British Columbia, Canada." *Forest Ecology and Management* 155: 387-398.
- Coates, K. D. and P. J. Burton (1997). "A gap-based approach for development of silvicultural systems to address ecosystem management objectives." *Forest Ecology and Management* 99: 337-354.
- De Chantal, M., K. Leinonen, et al. (2003). "Early response of *Pinus sylvestris* and *Picea abies* seedlings to an experimental canopy gap in a boreal spruce forest." *Forest Ecology and Management* 176: 321-336.
- Domisch, T., L. Finér, et al. (2000). "Growth, carbohydrate and nutrient allocation of Scots pine seedlings after exposure to simulated low soil temperature in spring." *Plant and Soil* 246: 75-86.
- Geiger, R. (1995). The climate near the ground. Vieweg textbook meteorology. R. Aron and P. Todhunter. Braunschweig, Vieweg: 457 - 500.
- George, E., B. Seith, et al. (1997). "Responses of *Picea*, *Pinus* and *Pseudotsuga* roots to heterogeneous nutrient distribution in soil." *Tree Physiology* 17: 39-45.
- Grassi, G. and G. Minotta (2000). "Influence of nutrient supply on shade-sun acclimatation of *Picea abies* seedlings: effects on foliar morphology, photosynthetic performance and growth." *Tree Physiology* 20: 645-652.
- Gray, A. N. and T. A. Spies (1996). "Gap size, within-gap position and canopy structure effects on conifer seedling establishment." *Journal of Ecology* 84: 635-645.
- Griffin, K. L., W. E. Winner, et al. (1995). "Growth and dry matter partitioning in loblolly and ponderosa pine seedlings in response to carbon and nitrogen availability." *Phytologist* 129: 547-556.
- Grossnickle, S. C. (2000). Ecophysiology of Northern Spruce Species: The Performance of Planted Seedlings. Ottawa, Ontario, Canada, NRC Research Press.
- Hannerz, M. and P. Gemmel (1994). Granföryngring under skärm - sammanfatning., Skogforsk.
- Holgén, P. (1999). Seedling Performance, Shelter Tree Increment and Recreation Values in Boreal Shelterwood Stands. Department of Silviculture. Umeå, Swedish University of Agricultural Sciences.
- Ingerslev, M. and L. Hallbäck (1999). "Above ground biomass and nutrient distribution in a limed and fertilized Norway spruce (*Picea abies*) plantation Part II. Accumulation of biomass and nutrients." *Forest Ecology and Management* 119: 21-38.
- Jentschke, G., D. L. Godbold, et al. (2001). "Nitrogen limitation in mycorrhizal Norway spruce (*Picea abies*) seedlings induced mycelial foraging for ammonium: implication for Ca and Mg uptake." *Plant and Soil* 234: 109-117.
- King, J. S., T. J. Albaugh, et al. (1999). "Stand-level allometry in *Pinus taeda* as affected by irrigation and fertilization." *Tree Physiology* 19: 769-778.
- Lascoux, M. and K. Lundkvist (1992). "Growth of 24 full-sib families of *Pinus sylvestris* at six relative nutrient addition rates." *Scandinavian Journal of Forestry* 7: 473-484.
- Malcom, D. C. and K. G. Ibrahim (1993). "Nutrient: productivity relations in plantation-grown Sitka spruce in Scotland." *Studia Forestalia Suecica* 191: 87-94.
- Proe, M. F., A. J. Midwood, et al. (2000). "Use of stable isotopes to quantify nitrogen, potassium and magnesium dynamics in young Scots pine (*Pinus sylvestris*)." *New Phytologist* 146: 461-469.
- Stoudtjesdijk, P. H. and J. J. Barkman (1992). Microclimate, vegetation and fauna. Knivsta, Opulus Press.
- Wayne, P. and F. A. Bazzaz (1993). "Birch seedling responses to daily time courses of light in experimental forest gaps and shadehouses." *Ecology* 74: 1500-1515.
- Örlander, G. and C. Karlsson (2000). "Influence of shelterwood density on survival and height increment of *Picea abies* advance growth." *Scandinavian journal of forest research* 15: 20-29.
- Örlander, G. and O. Langvall (1997). Markberedning och plantering. Skogsvårdsorganisationens årskonferens, Meddelande - Skogsstyrelsen nr 2:31-36.

