

Tree variables related to growth response and acclimation of advance regeneration of Norway spruce and other coniferous species after release

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Abstract

Modern forestry has been evolving towards multiple-use of forests and maintenance of biodiversity. Interest in integrating natural forest dynamics into management planning and silvicultural practices has increased as a result of concerns related to biodiversity values and maintaining ecological functions in managed forests. Taking advantage of naturally formed advance regeneration to create a new forest is one way of emulating natural forest dynamics, especially in spruce forests. However, efficient use of advance regeneration requires knowledge about factors influencing their performance. Light is important for growth and for crown, shoot and needle morphology of Norway spruce (*Picea abies*). Crown morphology varies from a conical and deep crown form in relatively high-light environments to the typical “umbrella” form in the understorey shade. Shoots and needles developed in shade are flatter and experience less self-shading than those developed in more light. Needle orientation is horizontal in shade and more vertically inclined in light. The number of nodal and internodal branches increases with increasing light. Tree shoot characteristics are strongly correlated and highly dependent on growing conditions, particularly light. There is a correlation between shoot and needle mass and other shoot variables of current and consecutive year’s growth. The strongest correlations are between length of the shoot and needle mass of the shoot, and the length of the shoot and number of needles on the shoot. Needle length was not as sensitive to the light environment. However, needle width and thickness increased with canopy openness. This paper presents a review of selected literature on the relationships between different tree variables and ecophysiological factors that influence the response and acclimation of Norway spruce advance regeneration to release. The results indicate that crown, shoot and needle characteristics could reflect the acclimation to light conditions and indicate the performance of advance regeneration after release.

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1. Introduction

Natural regeneration is attracting more interest as biodiversity, wildlife habitat preservation, and recreation are increasingly important goals of ecosystem management. Promoting the establishment and growth of advance regeneration offers several advantages. Advance regeneration that responds to release with increased height and diameter growth provides immediate stocking, shade for subsequent seedlings, an aesthetically pleasing landscape, protective cover for wildlife, and soil protection (Ruel et al., 2000). Furthermore, the use of advance regeneration reduces rotation length and

silvicultural costs (Ferguson and Adams, 1980; Lähde et al., 1999; Jeansson et al., 1989).

Silviculture based on the dynamics and structure of natural forests is called nature-oriented, ecologically oriented, or close-to-nature. Single-tree or group-selection harvests emulates the small-size gap disturbance that has been suggested as an important regeneration mechanism, for example in natural Norway spruce forests of Northern Europe (Kuuluvainen, 2002). Selection cutting focuses on individual trees or groups of trees, and seed-tree or shelterwood cutting systems operate at the stand level in diversity-oriented silviculture (Lähde, 1992; Lähde et al., 1999). The selection system aims at stand structures that consist of seedlings and trees of all ages. The intent is to cut both large and small trees (Jeansson et al., 1989). Trees removed in single-tree selection are replaced by natural advance regeneration (Lundqvist and Fridman, 1996; Dobrowolska, 1998). The use of advance regeneration is not limited to

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selection cutting systems; where even-aged systems, such as clearcutting or shelterwood cutting, are used, advance regeneration can be relied on if care is taken to protect the saplings during the logging operation.

The use of advance regeneration in silviculture requires that enough saplings establish under the canopy, and that they are able to respond favourably to subsequent canopy openings created by disturbance (an abrupt change in the forest biota and environment, *sensu* Frelich, 2002). The success of advance regeneration varies with the type of disturbance. In boreal forests, various types of small-scale and large-scale disturbances occur, which create openings in forest stands. Disturbances are important in the development of a new stand, since they create growing space by eliminating plants that previously occupied it. Disturbance events such as windstorms, avalanches, or logging operations, which do not completely destroy the forest floor, allow advance regeneration to gain a competitive advantage. When released from overstorey competition by a windstorm, advance regeneration spreads into the newly available growing space and can form a new stand. However, tree responses vary with the interaction between the species and the disturbance (Oliver and Larson, 1996). Both shade-tolerant and shade-intolerant tree species can be found in openings created by a disturbance event (Kneeshaw and Bergeron, 1996), and the composition of the resulting stand depends on how quickly the shade intolerant species can re-establish on the available growing space versus how quickly the advance regeneration can resume growth after release.

Acclimation and further development of advance regeneration after disturbance depend on the properties of the forest environment prior to disturbance and the type of disturbance (e.g., fire) (Tesch and Korpela, 1993; Man'ko, 1967, 2005). Therefore, several models that include different site factors have been developed to model the growth of advance regeneration of Norway spruce (Nyström and Kexi, 1997; Valkonen, 1997). Numerous studies in boreal forests have focused on soil conditions (Brang, 1998; Kneeshaw et al., 2002) and seedbed characteristics (Kneeshaw and Bergeron, 1996; Lieffers et al., 1996; Rooney and Waller, 1998; Cornett et al., 2001; Hanssen, 2003; Brang, 1998; Kneeshaw et al., 2002). Survival of the established saplings, however, depends on the available light and current growth rate (Claveau et al., 2002; Kobe and Coates, 1997). The role of competition has been explored in several studies (Kneeshaw and Bergeron, 1996; Hanssen, 2003; Nilson and Lundqvist, 2001; Duchesneau et al., 2001; Tesch et al., 1993; Grassi and Giannini, 2005).

The species-specific ecophysiological characteristics and their growth pattern determine the response of individuals of advance regeneration to disturbance events. In addition, the acclimation response of advance regeneration reflects growth performance prior to the release. Species that can establish as canopy trees from advance regeneration must have characteristics that enable them to survive in the deep shade of the overstorey and to respond favourably to the increasing light after the overstorey is disturbed. Shade-tolerant tree species normally have low leaf-mass-specific maximum photosynthetic rate and a respiration rate that goes with low mass-specific leaf

nitrogen content, high leaf longevity, and low relative growth rate when small, they also are capable of slow growth in adverse conditions with limited root growth (Reich et al., 1992, 1998a; Walters and Reich, 2000; deLucia et al., 1999). As the light reaching the saplings increases, these traits make them less able to compete in new conditions. However, low leaf-specific-net productivity may be compensated for by high leaf longevity, so that as the tree grows, the productivity of these shade-tolerant species may become more comparable to that of species with more efficient but shorter-lived leaves (Reich et al., 1992), thus allowing faster growth. The acclimation, however, is slow because it involves substantial change in leaf size.

Trees with very different rankings in shade tolerance seem to react similarly to changes in light climate (Reich et al., 1998a,b). Important variation in the physiological parameters of productivity depends on the nutritional status of the leaves. Thus changes in growth allocation in different parts of the tree in combination with altered soil and light conditions strongly influence tree growth response following release (Claveau et al., 2002; Kneeshaw et al., 2002). It can take several years after release for secondary (diameter) growth to occur on a tree (Youngblood, 1991). Kneeshaw et al. (2002) found that height growth does not respond immediately after release, but growth reaction is first seen in roots. They also reported that changes in allocation patterns from aboveground to belowground tissues may vary with climate and degree of overstorey removal. These findings are in agreement with the suggestion that trees try to maintain balance between their crown and root system functions (Nikinmaa, 1992). An increase in the growth of structural roots is also believed to counterbalance sway and prevent blowdown (Coutts, 1987). As relative growth rate and size increases, wood versus leaf allocation starts to become a more important determinant of the sapling performance (Mäkelä, 1988; Nikinmaa et al., 2003).

Numerous variables have been tested to explain the mortality and growth of advance regeneration after release. The most frequently proposed attributes are height, age, live crown ratio, and height or diameter growth before harvest (Ruel et al., 1995). Previous growth and growth tendencies of the tree have been used in empirical individual-tree growth models to predict subsequent growth (Pukkala and Kolström, 1991). However, leaf and needle morphology and crown architecture also can characterize the relative growth and acclimation to new conditions (Parent and Messier, 1995; Reich et al., 1998a). Combining these structural characteristics with plant physiology may allow us to develop predictive tools that would facilitate derivation of practical recommendations for the management of advance regeneration. As forest managers learn more about species' success in regenerating after disturbances, they can emulate disturbance patterns in forest management decisions (Fujimori, 2001; Wei et al., 2003; Jögiste et al., 2005).

In boreal Europe, Norway spruce is the only species with characteristics that allow the use of advance regeneration in its silviculture. This paper reviews selected literature on the relationships between different tree variables and ecophysiological factors that influence the response of advance regeneration of Norway spruce and other coniferous species

to release. The particular questions of interest are how Norway spruce compares to other species in its acclimation to understorey conditions and subsequent release, and how these features could be used to predict the sapling performance after release.

2. Review of literature

2.1. Canopy and sapling light availability

The density of a stand's canopy influences the light conditions (light availability) in the understorey. The amount of light received by understorey is an important factor for seedling establishment, survival and growth. Small saplings of sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) had light compensation points as low as at 1–2% of full sunlight, although the bigger saplings had considerably higher light requirement (e.g., Messier and Nikinmaa, 2000). In general, at least 20% of full sunlight is required for trees to reach the dominant crown layer (Barnes et al., 1998). Norway spruce is a shade-tolerant species that can exist as advance regeneration under the dense canopy of a mature forest stand (Jeansson et al., 1989; Valkonen et al., 1998). Norway spruce can establish under light demanding species, e.g., birch (Rubtsov et al., 2005). Natural death or a windthrow of single trees or groups of trees in the forest stand creates a canopy opening (canopy gap) that favours the establishment of natural regeneration and the existing advance regeneration (Hytteborn et al., 1987; Leemans, 1991; Coates, 2002). Norway spruce is one of the most common tree species to fill in gaps in forests of Northern Eurasia (Liu and Hytteborn, 1991; Drobyshev, 1999).

2.2. Crown properties

Lesinski and Sundkvist (1992) studied the crown morphology of Norway spruce advance growth and found the most frequent (52%) was symmetrical and conically shaped crown. Two other types were crowns that were divided into a higher and a lower part, separated by a branchless portion of stem, and a symmetrical, short, wide and dense crown (umbrella form). Grassi and Giannini (2005) showed the importance of light on growth and morphology of crowns, shoots and needles of Norway spruce and silver fir (*Abies alba*) saplings. In both species, crown morphology varied from a conical and deep crown form in relatively high-light environments to the typical “umbrella” form in the understorey shade. The form of trees in low light environments (understorey) is such that yearly branch increment is greater than height increment; hence crown width is frequently greater than 150% of stem height and three times crown depth (Tucker et al., 1987). Similarly, shoots and needles developed in shade are flatter and with less self-shading than those developed in light (Grassi and Giannini, 2005). Norway spruce crown types are showed in Figs. 1 and 2.

In understorey trees, needle and branch angles are almost completely horizontal and the crown is broad and shallow (O'Connell and Kelty, 1994). Trees have an arrangement of foliage that nearly maximizes total daily photon flux density on



Fig. 1. Heavily shaded Norway spruce with “umbrella” crown type.



Fig. 2. Open-grown Norway spruce (developing conical, regular crown).

the foliage from directly above the sapling. Due to longer light beam path length with lower angles, only a small proportion of light passes through the canopy and therefore the light climate is dominated by light from directly above the saplings

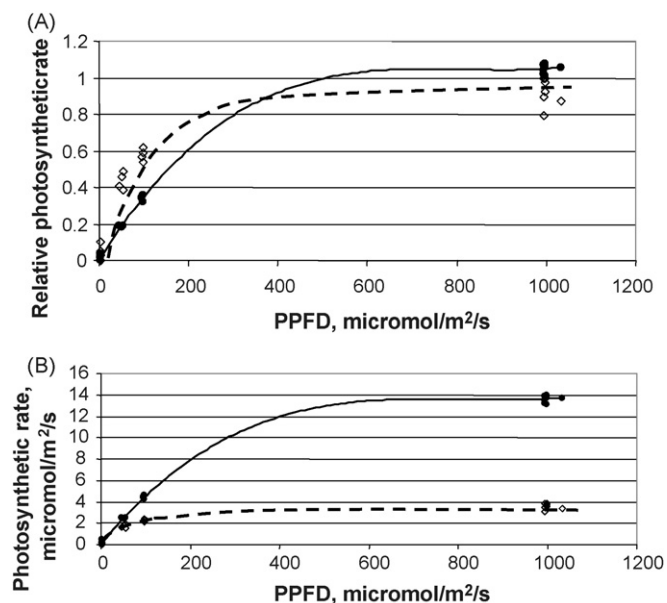


Fig. 3. Norway spruce photosynthetic rate relative to maximum rate (A) and photosynthetic rate (B) at the top of the tree crown (solid line and filled diamonds) and at the lower canopy (dashed line and open diamonds). PPFD is photosynthetic photon flux density.

(Duchesneau et al., 2001; Grassi and Giannini, 2005). On the sun-acclimated trees (open-grown trees) there is substantial self-shading within crown for any given shoot, with the exception of the topmost part of the tree (Tucker et al., 1987). Fig. 3 demonstrates Norway spruce relative photosynthetic rate and photosynthetic efficiency of shoots with different acclimation (different positions in tree crown; original data).

Internodal branches are important to increase the total foliage area in a high-light environment. Duchesneau et al. (2001) found that 25% of full sunlight was required to produce at least one internodal branch in balsam fir (*Abies balsamea*). Also, the number of nodal and internodal branches increases with photosynthetic photon flux density in this species (Parent and Messier, 1995). In contrast to spruce, Scots pine (*Pinus sylvestris*) advance regeneration increases branch growth after release, albeit with delay (Sundkvist, 1994). Similarly, Kneeshaw et al. (1998) found that an increase in the number of branches produced did not occur until 2 years had passed in Jack pine (*Pinus banksiana*) and Douglas-fir (*Pseudotsuga menziesii*). Long-term response to a prolonged increase in light in spruce would include an overall increase in the number of branches produced, in addition to increases in height growth and the ratio of leader to lateral branches (Kneeshaw et al., 1998).

2.3. Effect of shading on shoot and branch properties

Leader-to-lateral branch ratio reflects changes in tree architecture and is in positive correlation with the amount of light received (Parent and Messier, 1995; Klinka et al., 1992; Kneeshaw et al., 1998). Balsam fir (*A. balsamea*) follows a similar growth pattern as Norway spruce. Understorey trees have a lower degree of apical control (O'Connell and Kelty, 1994). In

high-light environments, trees produce longer leaders relative to lateral branches than do trees in low light (Chen et al., 1996). Ratios greater than 1 occur when leaders are longer than the average of lateral branch lengths and any increase in the ratio from 1 year to the next year reflects a change in architecture towards a form more adapted to height growth. Grassi and Giannini (2005) found that the last 3 years' average apical dominance ratio (ADR) is the simplest indicator for Norway spruce of the light conditions in which the tree is growing. A value of ADR = 1, corresponding to a relative irradiance of about 15–20%, may be used as a simple threshold to evaluate whether a sapling is likely to be considered light-stressed. This parameter is easy to measure and in the examined conditions does not change significantly with sapling height or competition (Grassi and Giannini, 2005). The growth differences between leader and lateral branches as a function of received light extends also to branch axes of different order. In heavy shading, the growth rate of the second-order lateral is greater than that of the first-order lateral (Greis and Kellomäki, 1981).

The different shoot characteristics are also strongly correlated and they depend on growing conditions, particularly light (Niinemets and Kull, 1995a; Stenberg et al., 1998; Stenberg et al., 2001; Messier and Nikinmaa, 2000). The length of the shoot and number of needles on the shoot ($r = 0.93$) and length of the shoot and needle mass of the shoot ($r = 0.91$) were the highest correlated shoot variables in trees that had been growing in a variable understorey environment (Metslaid et al., 2005a). Niinemets and Kull (1995b) found that needle number per unit shoot length increases with increasing irradiance and total tree height. The shoot length slightly decreases with increasing tree height, but not significantly, and shoot length did not correlate with the needle number per unit shoot length (Niinemets and Kull, 1995b). The average shoot size in the understorey was smaller in heavier shade (Metslaid et al., 2005b). The average volume of the needles decreased more than the shoot needle mass with increasing shade, indicating that shoot size was less influenced than needle properties. Metslaid et al. (2005a) found that bigger trees tended to have bigger shoots, but the correlation of tree diameter increment with different variables of shoots of the same year was only moderate (Metslaid et al., 2005b). In trees with similar height, those with larger diameter growth also had greater foliage mass.

Sun shoots typically have more needle area per unit shoot length than do shade shoots, and the orientation of needles around the shoot axis is more uniform. Needle inclination is an important stand characteristic as it influences shoot light absorption (Niinemets and Kull, 1995b). In shade shoots, needles are displayed mainly at the sides and the shoot appears to be flat (Stenberg et al., 1999). The vertical inclination of the needles depended on prevailing light conditions. In heavy shade the needle inclination was about 5° , and in the open, 45° (Greis and Kellomäki, 1981).

2.4. Effect of shading on the characteristics of needles

Specific needle area, i.e., needle area per unit biomass, and the ratio between needle thickness and width, can be used as

indicators of needle structure. It is also one of the principal mechanisms by which different tree species acclimate to variations in light conditions (Reich et al., 1998a,b). Greis and Kellomäki (1981) found that needles were thin and wide in heavy shading; needle width was nearly three times greater than needle thickness when the light intensity was 25% of that in the open area. In an open, free-to-grow environment, the ratio between needle thickness and width was almost 1, making the shape of the cross-sectional cut of the needles resemble a square.

Duchesneau et al. (2001) showed that light availability does not substantially affect needle surface area of a single needle, confirming earlier reports for a wide range of plant species (Niinemets and Kull, 1994). At the same time, specific leaf area increased in low-light environments (Chen et al., 1996). This kind of morphological acclimation usually results in a variation of leaf thickness or specific density of needles. Thinner needles create a bigger surface area for photosynthesis with the same structural investment by the plant, which is advantageous for trees in scarce light conditions (Chen et al., 1996). At the same time it is advantageous to invest in more photosynthetic capacity and area where relative irradiance is high, which leads to a bigger needle number per unit shoot length (Niinemets and Kull, 1995b).

Needle length is not sensitive to the light environment, whereas needle width increases with light availability (Stenberg et al., 1999; Niinemets and Kull, 1995a). In conifers needle thickness generally increases with increasing irradiance (Niinemets, 1997). Stenberg et al. (1999) found that needle width and thickness increased with canopy openness. However, no significant relation was found between needle thickness and irradiance. In Norway spruce, needle width is more responsive to irradiance than needle thickness. Needle width increased significantly with the relative amount of penetrating diffuse solar radiation. Thus the needle thickness/needle width ratio decreased, but the ratio of total and projected needle surface area increased. Needle thickness was found to be lower in shade needles than in sun needles, and the ratio of needle thickness to width was bigger for sun needles (Niinemets and Kull, 1995a; Niinemets, 1997).

Total and projected needle surface areas and needle lengths were not significantly related to irradiance. Needle dry weight per total surface area and per projected surface area increased with increasing relative amount of penetrating diffuse solar radiation and greater tree height. Needle density increased with total tree height. There was no significant correlation between height of needle location and stand density (Niinemets and Kull, 1995a).

Niinemets and Kull (1995a) found no correlation between tree height and relative amount of penetrating diffuse solar radiation, but they found significant correlation between sapling height and light availability. The needle mass per area increases with increasing irradiance and total tree height (Grassi and Giannini, 2005). Also, needle length tends to increase with total tree height, but not significantly (Niinemets and Kull, 1995a). Niinemets and Kull (1995a) reported that the amount of photosynthesizing tissue per unit leaf (needle)

weight decreased with increasing tree age or height. Older Norway spruce trees grown in open areas have lower total needle surface area and weight-based photosynthetic capacities than younger trees (Kull and Koppel, 1987).

2.5. Acclimation to release

Norway spruce is able to respond to its current environment by modifying needle structure and functions to maximize exploitation of light resources. Therefore high phenotypic plasticity is one of the most important characteristics of Norway spruce. This growth pattern enables Norway spruce to survive in a variety of sites, but at the expense of a reduced growth rate even in the presence of a rich supply of resources (Greis and Kellomäki, 1981). One explanation could be that understorey saplings sacrifice height and also diameter growth in order to allocate a higher percentage of current-year production to foliage and shoots (O'Connell and Kelty, 1994).

Shoot growth and the number of needles per shoot are influenced by temperature conditions during the previous summer when the buds were formed; temperature during the current summer affects the length of the needles (Salemaa and Jukola-Sulonen, 1990).

Metslaid et al. (2005b) studied the growth reaction after stand opening. After understorey release, the shoots were systematically bigger in the latter of 2 consecutive years. Larger shoots grew more than small ones, while the relative growth remained constant between shoots but was subject to annual variation (Metslaid et al., 2005b). Shoot growth had fully recovered by the third year. By the end of the fifth year, the whole shoot population seemed to be growing bigger than the similar population during the previous year. It also seemed that by year 4 after the release, there was no further increase in shoot growth. Due to correlation of shoot properties within the same year and between consecutive years the shoot properties have high correlation between consecutive years (Jögiste and Metslaid, 2002; Metslaid et al., 2005b).

Tucker et al. (1987) found that Pacific silver fir (*Abies amabilis*) branch growth recovered in the second growing season, although height growth recovered only in the third growing season following release. This lag of height growth behind branch extension growth may be due to: (1) the time required for physiological adjustment by the apical bud and the subsequent restoration of apical control; (2) an increase in the quantity (or proportion) of sun foliage; (3) the restoration of other functional balances within the tree. Within 2–5 years, however, released trees showed larger branch and leader increments than they did before release. Our studies indicate that the recovery rate in Norway spruce was very similar to that of Pacific silver fir (Tucker et al., 1987).

Due to correlation between the shoot size and properties, the reaction of saplings to release can be predicted from tree size and the growing environment (degree of shading) in the understorey and the shoot size and shoot growth after understorey release, along with sapling size and competition from surrounding plants (Metslaid et al., 2005a). Sapling age also may have a role in acclimation, especially in trees that have

very long-lived leaves such as Norway spruce. Niinemets and Kull (1995a) found that needle structure changed more rapidly in younger plants (1–10 years old) than in older plants (over 10 years old).

3. Conclusions

Disturbance events and clear-cut logging often release advance regeneration of various size and age distributions. When released from overstorey competition by a windstorm or a regeneration cut, advance regeneration occupies the newly available growing space and forms a new stand. Acclimation and further growth of advance regeneration trees after a disturbance event depend upon several environmental factors, and light is one of the most important factors for seedling establishment, survival and growth. Shoot and needle morphology can reflect the relative growth and acclimation to new environmental conditions. Therefore, ecophysiological characteristics can be used to describe the response of advance regeneration trees to release.

Norway spruce exhibits acclimative characteristics similar to many other shade-tolerant tree species. The conical crown shape of open growing conditions is reversed to the umbrella form upon loss of apical dominance with decreasing light. The apex versus branch growth has been suggested as an efficient indicator of the shading experienced by a tree, and the potential to respond to release is similar for Norway spruce (Grassi and Giannini, 2005) and balsam fir (Parent and Messier, 1995). Shoot growth is highly correlated with different shoot characteristics, but they are all sensitive to light conditions. As there is a high correlation between shoot and needle mass and other shoot characteristics of current and consecutive years after release, the structural modifications resulting from shading in the understorey have long-term impact on sapling performance after release. Models that use these characteristics as additional predictors of sapling growth better predicted sapling performance after release than models using just size and competition information (Metslaid et al., 2005a).

The fast acclimation of the newest shoots of Norway spruce to the release seemed to take place within 4–5 years after release (Metslaid et al., 2005b) and similarly for silver fir (Tucker et al., 1987). However, the whole plant response is slower in older saplings as the renewal of the whole tree needle properties is slower in older than younger plants (Niinemets and Kull, 1995a). Tree size and age are correlated in similar light conditions but lose the connection in variable light environments. However, as shoot characteristics are able to indicate variation in the shading that is experienced, models that include indicators of shoot properties, sapling size and competition after release are more powerful in predicting the sapling recovery after release than just those using, for example, size as a predictor. As these variables are included in the analysis it is clear that the bigger the saplings that have been in strong shade, the slower the growth response after release (Metslaid et al., 2005a).

Advance regeneration plays an important role in the regeneration strategies used in forest management. Promoting

the establishment and growth of advance regeneration offers several ecological and economic advantages. Crown, shoot and needle characteristics reflect the acclimation of advance regeneration trees to different light conditions, and an examination of them can help to predict the performance of trees after release. A better understanding of the response and acclimation of Norway spruce advance regeneration and natural processes within forest stands could improve the ability to manage ecosystems in the future, and improve existing silvicultural systems. Studies that examine the growth response of advance regeneration and processes within stands can form the basis for developing silvicultural systems that emulate the natural dynamics of forest ecosystems.

Practical methods to address the dynamics of growth response and acclimation of advance regeneration would be a useful tool for forest management. The capacity of Norway spruce to react to the greater availability of light influences establishment success and stand formation. Gap development creates a situation in which advance regeneration trees of different acclimation and development status occur in groups. The most viable trees in these dense patches can be identified based on tree size, crown properties, and shoot and needle characteristics (lateral and leader lengths, needle number and mass per unit shoot length). Dense groups of advance regeneration need to be tended and competition by other advance regeneration and deciduous trees removed. A practical implication would be to apply selection cutting, focusing on single trees or groups of trees, or a shelterwood cutting system. In the areas where different regeneration cutting systems (clear-cut, single-tree selection, etc.) are used, the advance regeneration can be saved during the logging operations.

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