



Seedling responses to changes in canopy and soil properties during stand development following clear-cutting



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ABSTRACT

The role of natural regeneration in silvicultural systems is attracting increasing interest, but much is unknown about how stand development after clear-cutting affects seedling regeneration. We looked at the impact of tree canopy and ground layer vegetation (i.e., 'stand type') as well as soil properties (i.e., 'soil origin' or stand from which soil originated) on survival and growth of *Pinus sylvestris* and *Picea abies* seedlings at three forest developmental stages, i.e., 4, 16 and 34 years after clear-cutting. To do this we transplanted soil cores between stands of different stages to separate the effects of soil properties versus canopy closure on seedling performance. We found that seedling survival of both species was highest when planted in the oldest stands independent of soil origin. *P. sylvestris* seedling growth responded to stand type but not soil origin, and biomass was highest at the youngest stand likely because of greater light availability. Meanwhile, although *P. abies* seedling root biomass responded to stand type, this species was mostly responsive to soil origin, with shoot and total biomass being greatest when seedlings were grown in soil originating from the oldest stands. These findings have implications for our understanding of tree regeneration of species that differ in their responsiveness to light and soil characteristics. The results can further inform forest managers about how to optimize survival and growth of seedlings by means of canopy regulation as well as provide information to assist the regeneration and development of multi-storied forest stands.

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1. Introduction

Sustainable forest management includes the harvest of trees, and subsequent forest regeneration, to ensure future forest cover and economic revenue. One of the most established and frequently used harvesting methods in the boreal region is clear-cutting (or clear-felling) (Lundmark et al., 2013). However, public demands require forest management to evolve towards a management that fulfills multiple functions and sustainability goals (Puettmann et al., 2009). These developments have led to discussions about alternatives to the clear-cut system (e.g., partial-cutting systems) that involve natural conifer regeneration without soil scarification, and maintenance of a greater density of living trees on site after logging (Hanssen, 2003; Puettmann et al., 2009; Kuuluvainen et al., 2012). The importance of natural regeneration, which includes careful logging around advanced regeneration, has been

recognized in at least parts of eastern Canada (Bergeron and Harvey, 1997; Harvey and Brais, 2002; Groot et al., 2005). Nowadays, there is also an increased awareness of the importance of natural regeneration in clear-cut systems in Scandinavia. Natural regeneration can help achieve governmental regeneration requirements, enhance timber quality by means of increased tree density, and increase genetic and species diversity (Ackzell, 1992; Ackzell et al., 1994; Lindén and Agestam, 2003; Mielikäinen and Hynynen, 2003). Despite the increased interest in natural regeneration in both clear-cut and alternative silvicultural systems, there remains a paucity of knowledge regarding the relative importance of the canopy, understory vegetation, and humus layer (Ponge et al., 1998) for the success of forest regeneration across different forest stand development stages.

Forest canopies and understory vegetation can exert facilitative or competitive effects on establishing seedlings, and these effects can change direction and magnitude during forest development (Callaway and Walker, 1997). Clear-cutting followed by site preparation causes disruption of the forest floor and a large shift in microclimate that involves higher temperatures and wind exposure due to tree removal (Økland et al., 2003). These factors have an immediate impact on understory species density and composition

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(Schmalholz and Hylander, 2011; Swanson et al., 2011). As the time after clear-cutting increases, the canopy closes and dwarf-shrub and moss biomass often increase, while grasses that are particularly abundant immediately after clear-cutting in Scandinavia eventually decrease (Hannerz and Hånell, 1997; Harvey and Brais, 2002; Tonteri et al., 2013; Stuiver et al., 2015). Light becomes limiting as a consequence of canopy closure which may negatively affect seedling performance (Lieffers and Stadt, 1994; de Chantal et al., 2003), but it can also suppress understory vegetation and thereby facilitate seedling performance (Kuuluvainen et al., 1993; Lieffers et al., 1999). Understory vegetation has frequently been shown to reduce seedling growth by competing for light and nutrients (Steijlen et al., 1995; Hörnberg et al., 1997; Jäderlund et al., 1997; Zackrisson et al., 1998; Mallik, 2003; Hyppönen et al., 2013). However, previous studies investigating these effects have often been limited to one specific stand development stage (typically a few years after logging) in production forests (Wagner et al., 1999; Palviainen et al., 2005; Prévost et al., 2010), or have been assessed across very large time ranges in natural forests (Wardle et al., 2008). The presence versus absence of a canopy and understory vegetation might also affect the water availability for the seedlings through differences in evapotranspiration, evaporation from the forest floor, air humidity and soil moisture in the stand (Jemison, 1934; Oleskog and Sahlén, 2000; Kreutzweiser et al., 2008; Blok et al., 2011). Therefore, a better understanding is required of the direct and indirect effects of canopy and understory vegetation on seedlings (Wagner et al., 2011) and how these effects change with forest development in production forests.

The disturbance effect of clear-cutting and subsequent changes in vegetation community composition during forest development can also affect soil properties (Johnson and Curtis, 2001; Frey et al., 2003; Prescott et al., 2003), thereby potentially affecting seedling regeneration. For example, in the short-term, clear-cutting is generally expected to increase mineral N concentrations in the soil (Olsson et al., 1996; Rosén et al., 1996; Prescott, 2005; Piirainen et al., 2007), because of increased N mineralization and nitrification rates and decreased uptake by vegetation (Jerabkova et al., 2011). However, decreasing or unchanged levels of mineral N have also been found after clear-cutting (Johnson and Curtis, 2001; Palviainen et al., 2004; Stuiver et al., 2015). These contrasting findings among studies are likely due to study or site specific factors (e.g., time after clear-cutting, size of clear-cut, vegetation type, soil type, or measurement techniques) and differences in harvesting and soil preparation methods (e.g., retention of slash or trees, mounding versus disc-trenching) that vary in soil disturbance severity (Jerabkova et al., 2011; Pötzelsberger and Hasenauer, 2015). While studies comparing pre- and post-harvest conditions are quite common (e.g., Olsson et al., 1996; Johnson and Curtis, 2001; Piirainen et al., 2007), fewer studies have addressed how soil nutrient availability changes with stand development following clear-cutting in the long-term (but see Kurth et al., 2014; Pötzelsberger and Hasenauer, 2015). For example, varying rates of litter input and decomposition may be influenced by changes in the overstory and understory vegetation during forest development after clear-cutting (Oechel and Van Cleve, 1986; Nilsson and Wardle, 2005), which can either increase or decrease nutrient turnover and availability (Turetsky, 2003; Blok et al., 2011; Jackson et al., 2013; Soudzilovskaia et al., 2013). Such changes are likely to have profound consequences for tree regeneration in N limited boreal forests (Tamm, 1991; Royo and Carson, 2006), but our knowledge of how changes in soil properties influence seedling performance relative to changes occurring in the canopy and understory vegetation remains limited.

In this study we used an established production forest chronosequence in northern Sweden consisting of three developmental stages after clear-cutting (Stuiver et al., 2015). The

chronosequence approach is a well-established tool for studying dynamics of plant community and ecosystem development, especially in systems such as ours in which sites of different ages follow the same trajectory and have a few dominant species (Walker et al., 2010). In order to test how tree seedlings (planted 8 weeks after germination) interacted with above- and belowground factors specific to different stand development stages, we performed a full factorial transplantation experiment. Specifically, we studied how *Pinus sylvestris* L. and *Picea abies* (L.) Karst. seedling survival, growth and allocation patterns responded individually and interactively to variation in canopy and soil conditions. For this study we had the following objectives. First we examined how tree seedling performance (survival and growth) responded to changes in canopy properties (notably light transmission) and vegetation biomass during forest development following clear-cutting. Second, we examined the response of seedling performance to changing soil properties with increasing time after clear-cutting. Third, we investigated whether effects of soil properties on seedling growth were greater when light was less limiting. We addressed these objectives using seedlings of each of two tree species, i.e., *P. sylvestris* and *P. abies*, that have contrasting relationships with soil fertility and light availability (Kuusela, 1990; de Chantal et al., 2003; Dehlin et al., 2004). As such, we predicted that changes in light across the chronosequence should be more important for *P. sylvestris* while changes in soil properties should be more important for *P. abies* because the latter is more shade tolerant (Kuusela, 1990; Kuuluvainen, 1994). Addressing these objectives in combination will provide a better understanding of the processes that determine seedling survival and growth, which is of particular relevance to natural regeneration which is growing in interest as a forest management practice in the Nordic region (Puettmann et al., 2009; Skogsstyrelsen et al., 2009).

2. Material and methods

2.1. Site description

This study was carried out along a chronosequence with 24 forest stands that varied in their year of initiation by clear-cutting. The stands were located in an area of 2500 km² in the surroundings of Arvidsjaur (65° 35'N–19° 10'E), northern Sweden on land owned by the forest company Sveaskog. The average annual temperature was 1.2 °C, the average July and January temperatures were 13.4 and –13.3 °C respectively, and annual precipitation was 542 mm over the period of 2002–2013 (Swedish Meteorological and Hydrological Institute, 2014). Stands were selected so that they had an equal site productivity index (which indicates the tree growth potential of the site), vegetation type (*Vaccinium myrtillus*; Hägglund and Lundmark, 1999), with an average slope of about 6°, and were on the same type of substrate, i.e., sandy silt glacial soil, with a deposit of unsorted glacial till. Prior to clear-cutting the mature forests were typically about 120 years old and dominated by *P. sylvestris* with an understory of *P. abies* (Stuiver et al., 2015).

The 24 forest stands were divided into three stand types based on their time since clear-felling ($n = 8$ in each) (Table A.1). These stand types were: (1) CC (clear-cut and recently planted with *P. sylvestris* seedlings, mean stand age 4 years), (2) PCT (pre-commercial thinning stands, mean stand age 16 years), and (3) T1 (first commercial thinning stands, mean stand age 34 years). All three stand types have been managed according to conventional forestry management practices, meaning that they all had been clear-cut, subjected to mechanical patch soil preparation (e.g., mounding with the exception of one stand in T1, which was superficially ploughed) and planted by the forest owner with *P. sylvestris*.

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