Forest Ecology and Management 430 (2018) 105–116

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Long-term development of natural regeneration in irregular, mixed stands of silver fir and Norway spruce

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ARTICLE INFO

Keywords:
Regeneration height
Regeneration density
Residual overstory
Structural diversity
Uneven-aged silviculture
Norway spruce
Silver fir

ABSTRACT

The timely establishment of natural regeneration of the preferred species after the death or removal of mature trees is essential in continuous-cover forestry. In the context of the gradual shift from even-aged and monospecific to uneven-aged and/or mixed forest stands, the limited availability of statistical models to predict seedling establishment, survival, and growth has increasingly become a bottleneck for forest management planning and, ultimately, a potential limitation to a wider adoption of alternative silvicultural approaches.

We investigated the development of top height and density of natural regeneration in 19 uneven-structured, mixed silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) H. Karst.) stands in southwestern Germany using long-term observations (35 years) from permanent plots. We used linear mixed-effects models to analyze the influence of overstory and understory-related variables on regeneration of fir and spruce.

The height of the five tallest juvenile trees per regeneration subplot and species increased significantly with diminishing canopy cover and increasing structural diversity of the overstory. However, competition exerted by tall juveniles substantially impacted the development of smaller neighbors, which were less able to profit from favorable overstory conditions. These results indicate that canopy cover and structural diversity need to be taken into account when modeling height development of juvenile trees in irregular stands. Importantly, these results also demonstrate the potential of silvicultural interventions to shorten the time period when terminal shoots are vulnerable to browsing.

Densities of juvenile trees displayed a unimodal relationship with the mean height of the regeneration. Fir and spruce densities culminated at a mean height of approx. 50 cm and decreased rapidly afterwards. This pattern indicates an early onset of competition within the regeneration layer. For both species, juvenile densities were unrelated to overstory structural diversity, yet they showed positive relationships with overstory density and site productivity.

Overall, fir juveniles developed faster in height than spruce juveniles. Even rather rapid group-shelterwood cutting regimes with complete canopy removal within two decades still favored fir regeneration. In addition, a high proportion of fir in the regeneration cohort had a stronger negative effect on spruce juvenile density than vice versa. Since spruce is less shade-tolerant than fir, it is likely that fir will dominate the future stand composition.

Overall, our models provide the basis to predict natural regeneration dynamics in structurally complex stands dominated by fir and spruce and to further evaluate alternative treatment scenarios.

1. Introduction

The gradual shift from even-aged monospecific to uneven-aged and/or mixed forest stands has intensified in recent years in the attempt to increase the resistance and adaptability of forests to ongoing global change (Pretzsch et al., 2017). Key to achieving and maintaining sustainable stand structures with “alternative silvicultural approaches” (*sensu* Puettmann et al., 2015) is a timely establishment of natural regeneration after the death or removal of mature trees, followed by survival and recruitment of the preferred species (Schütz, 2002).

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https://doi.org/10.1016/j.foreco.2018.07.055
Received 7 May 2018; Received in revised form 18 July 2018; Accepted 29 July 2018

However, in spite of the importance of natural regeneration for "alternative silviculture" and the long tradition that such practices enjoy in some parts of the world (Gayer, 1886; Liocourt, 1898; Biolley, 1901), the existing body of research concerning regeneration is considerably smaller than that which refers to mature trees.

This knowledge gap may be attributable to the fact that natural regeneration data have always been costly and challenging to collect, given the high spatial and temporal stochasticity of the underlying processes (Miina et al., 2006; Weiskittel et al., 2011). This high stochasticity may be partly responsible for the low predictive ability of many existing regeneration models (Weiskittel et al., 2011). However, traditional sources of regeneration data, such as forest inventories and regeneration experiments, also have important limitations. Inventories are usually geographically representative and unlikely to be dominated by exceptional weather conditions, yet they often provide little insight with regard to important determinants of regeneration such as past management, time since regeneration, regeneration origin or development in the absence of browsing (Weiskittel et al., 2011). In contrast, regeneration experiments have a more limited spatial extent, but the possibility to control a wide range of expected conditions makes them more suited for building regeneration models (Miina et al., 2006).

Ideally, regeneration models based on long-term experiments should help us understand how various management scenarios impact the speed of regeneration establishment and growth, as well as the likelihood that, and proportions in which, certain species will be recruited into the canopy (Hasenauer and Kindermann, 2006; Miina et al., 2006). However, modeling regeneration growth dynamics in mixed forest stands poses considerable difficulties even when suitable data are available (e.g. Vickers et al., 2014). Important reasons are that the biological processes underpinning growth dynamics in mixed regeneration cohorts are intrinsically complex (i.e. they reflect species-specific physiological and morphological adaptations to limiting factors, e.g. light) and interact over various temporal and spatial scales.

In natural temperate forests, gaps resulting from small-scale disturbances are the most frequent source of variation for understory light, temperature, soil mineralization and humidity. The amount and quality of available light may vary depending on gap size, the height of the surrounding canopy, solar angle, latitude, and aspect (Canham et al., 1990). Because light levels beneath undisturbed canopies may represent only 1–6% of full sunlight (Canham et al., 1990), increases in light levels in gaps are expected to stimulate the germination of seeds and drive the growth of established seedlings and saplings (Bazzaz, 1996). In particular, single-tree selection and shelterwood regimes recognize the importance of managing light environments to control understory growth and regulate height differentiation among species (Stancioiu and O'Hara, 2006; Petrițan et al., 2009).

Overstory trees are expected to impede the survival and growth of juvenile trees particularly by overhead shading (Oliver et al., 2005). Different measures of overstory competition have been successfully used to predict height and density development of juvenile trees (Hasenauer and Kindermann, 2006). However, other influences such as root competition exerted by the overstory trees might also play an important role. As a result, there is still considerable uncertainty on how to best quantify overstory impacts on regeneration survival and growth (Oliver et al., 2005) and it is unlikely that this dependency can be described using a single metric (Lhotka and Loewenstein, 2008).

Traditional metrics of stand density such as stand basal area or volume are often employed in regeneration models, yet they generally show weak relationships with regeneration development in uneven-structured forest stands (Chrimes and Nilson, 2005). Sometimes the growth-limiting effects of overstory density may be emphasized by slightly modifying the analytical approach. For instance, focusing exclusively on the fastest growing juveniles in a regeneration cohort may lead to such an outcome (Vickers et al., 2014) possibly due to limiting the confounding effect of competition within the regeneration cohort.

However, the main issue with traditional stand density metrics is that they fall short in irregular stands by failing to account for heterogeneous horizontal and vertical distributions of canopy gaps and biomass (Beaudet et al., 2011; Lochhead and Comeau, 2012; Vickers et al., 2014). Previous work suggests that vertical canopy structure may act as a regulator of environmental factors that influence regeneration development and that it should be accounted for when modeling regeneration dynamics (Beaudet et al., 2011; Lochhead and Comeau, 2012).

Mixed mountain forests of fir-spruce (possibly with some admixed beech; *Fagus*) represent an ecologically and economically important forest type in Europe (e.g. Hanewinkel, 2002). Currently, Norway spruce (*Picea abies* (L.) H. Karst.; "spruce") is the most widespread and economically most important species in Europe. However, its prominent role may change in the future since spruce is expected to become unsuitable over large areas of its current, human-influenced distribution range even under moderate climate change scenarios (Hanewinkel et al., 2013).

In contrast, the current economic importance of Silver fir (*Abies alba* Mill.; "fir") is ranked much lower than that of spruce. However, this rating reflects the relatively small area currently occupied by fir rather than its economic potential, which is actually similar to spruce. Importantly, while fir is certainly not a drought-tolerant conifer, compared to spruce it might display a better potential to adapt at least to moderate climate warming expected at mid-term for central Europe (Vitali et al., 2017, 2018). Additionally, fir is clearly less susceptible to storm damage (e.g. Albrecht et al., 2012) and considerably less threatened by aggressive attacks from bark beetles (e.g. Frehner et al., 2005). In contrast to spruce, fir's current distribution still generally reflects its native distribution range, which has been only slightly extended through forest management. In addition, fir has been mostly naturally regenerated and therefore fir stands and populations can be in many cases considered indigenous.

Considering the poor outlook of spruce under climate warming scenarios, it seems sensible to substitute portions of the vulnerable spruce with the expectedly more robust fir and/or to increase the contribution of fir in mixtures. This notion would be further supported if continuous-cover forest management regimes are to be favored (Brang et al., 2014), which is certainly the case for publicly owned forests in southwest Germany (Kohnle and Klädtke, 2010). Under such regimes with long regeneration periods, species' proportion in mixed regeneration cohorts may be regulated by altering canopy cover and thus the provisioning of light in the understory. Although both species can establish and survive under low light conditions (Hunziker and Brang, 2005), fir is notably more shade tolerant than spruce (Grassi and Bagnaresi, 2001). Consequently, this difference may benefit fir in shaded understories and lead to a competitive advantage for spruce under more open conditions (Stancioiu and O'Hara, 2006).

The purpose of this study was to identify drivers of juvenile height and density development in the natural regeneration of uneven-structured mixed stands of fir-spruce. Juvenile height provides an informative measure for forest practitioners and facilitates modeling height development trends. Juvenile density is especially interesting in connection to average juvenile size, since it allows insights into the self-thinning trajectories of natural regeneration cohorts. The specific objectives included (1) examination of height and density development of juvenile trees in relation to overstory attributes (density and structural diversity) and competition within the regeneration cohort, (2) estimation of the time needed by juvenile trees to reach heights at which they escape browsing (here, for comparative purposes, we used for a subjective threshold of 2 m), (3) evaluation of differences in height and density development between fir and spruce.

2. Material and methods

2.1. Study area

The five experimental sites used in this study are located in southwest Germany along an elevation gradient of 500–1000 m.a.s.l. and are