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Forest regeneration dynamics following bark beetle outbreak in Norway spruce stands: Influence of meso-relief, forest edge distance and deer browsing

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ABSTRACT

Management of Norway spruce monocultures in Europe is becoming increasingly difficult due to frequent natural disturbances. Their transformation could be especially challenging if several disturbances interact. In 2003 a spruce bark beetle outbreak damaged large tracts of spruce bottomland successional forest in southeast Slovenia where overabundant ungulate populations are present. In openings (5.4–7.5 ha in size) in four salvaged forest compartments, we studied the effects of meso-relief, forest edge, seed trees and fencing on vegetation succession and tree regeneration. In 2005 and 2013 we sampled seedling density on 240 plots according to height class and species. In the second inventory we also assessed distance to seed trees and on a subsample of the plots the coverage of vascular plants. The results indicated sufficient natural regeneration and niche partitioning among species groups, with Norway spruce seedlings being more successful at stand edges, pioneers and anemochorous broadleaves in gap centres, and zoochorous broadleaves on plateaus as opposed to sinkholes. Seedling density of all anemochorous broadleaves was higher closer to seed trees. Spruce seedling abundance was negatively associated with the cover of herbaceous vegetation and that of pioneer trees with shrubs. Fencing resulted in significantly greater density, height and coverage of seedlings as well as a higher share of broadleaves. While bark beetle outbreak triggered regeneration of broadleaves, overbrowsing acted in the opposite direction by facilitating spruce. Thus, to accelerate successional development and to prevent a spruce dominated alternative ecosystem state, a significant reduction in deer abundance is needed. To safeguard seed sources, promote seed dispersal by encouraging perches and shelters, and preserve potential habitats, some damaged trees should be retained during salvaging operations.

1. Introduction

Natural and anthropogenic environmental changes increase the frequency and severity of forest disturbances (Seidl et al., 2011). In Europe, pure Norway spruce (*Picea abies* (L.) H.Karst., hereafter spruce) stands are particularly vulnerable to biotic and abiotic disturbance (Klimo et al., 2000; Schelhaas et al., 2003). This is due to tree architecture (e.g. shallow root system), wood properties, delayed recovery after wounding when compared to broadleaves and frequent single-layered stand structure (Ott et al., 1997; Mason, 2002; Stokes et al., 2005). The most common natural disturbances that affect spruce monocultures in Europe are bark beetle outbreaks and windthrows (FE/UNECE/FAO, 2011).

Conversion of spruce monocultures to uneven-aged mixed stands improves their resistance to natural hazards (Schütz et al., 2006; Griess et al., 2012). In this regard, gradual transformation is an interesting alternative to seeding or planting from an ecological and economic perspective (Kenk and Guehne, 2001; Schütz, 2002). It is based on thinning and natural regeneration that includes spruce, which may partially serve as a nurse plant and partially as a future crop tree, depending on the site conditions. However, natural regeneration of spruce monocultures is challenging due to eutrophication or acidification of forest soils, which is influenced by stand, soil and climate characteristics (Fanta, 1997; Klimo, 2002). Openings in the canopy layer cause the accelerated decomposition of soil organic material, release of nutrients and development of competitive ground vegetation (Diaci, 2002; Rothe et al., 2002). Spruce seedlings grow slowly and are more inhibited by competitive ground vegetation than broadleaves (Ellenberg, 1988). In addition to disturbed nutrient cycling, a lack

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of seed trees of the original forest communities also significantly delays conversion (Mansourian et al., 2005).

Natural disturbances compound the problems impeding conversion. Natural regeneration is especially hindered by the development of competitive ground vegetation (Wohlgemuth et al., 2002; Fischer et al., 2002; Rammig et al., 2007; Jonasova et al., 2010). These plant species help conserve nutrients, prevent erosion and may facilitate the establishment of dendroflora. However, some long-lived species (e.g. *Crataegus* sp.; *Corylus* sp.) may also slow progression towards late successional forest (see also Jonasova and Prach, 2008; Heinrichs and Schmidt, 2009). After disturbances, regeneration is more successful on special, safe microsites, particularly on gap edges, rocky outcrops, elevated positions, mineral soil and decomposed deadwood (Eichrodt, 1969; Dai, 1996; Baier et al., 2007; Hanssen, 2003; Vodde et al., 2011). Salvage logging may increase areas with exposed mineral soils, but it also removes deadwood, an important spruce seedbed (Svoboda et al., 2010), and may damage advance regeneration (Lindenmayer et al., 2008). On salvaged plots in particular, ground vegetation and pioneer tree species are often more abundant compared to spruce and other broadleaved species; thus, forest recovery may be delayed (Jonasova and Prach, 2004; Jonasova and Matejkova, 2007; but see Ilisson et al., 2007 for windthrow). After sanitary felling, cleared areas are often replanted. Due to the low costs, high survival rate and low palatability, spruce is often planted again as a nurse tree, although natural succession may lead to equal or higher density, composition and quality of tree regeneration.

Restoration of forest protection and economic functions is more difficult when several disturbances act simultaneously or in short time intervals (Rammig et al., 2007; Bottero et al., 2013). In many parts of the world (Côté et al., 2004; Hester et al., 2006), and particularly within Central Europe, overbrowsing constitutes a chronic disturbance. Experimental studies in eastern deciduous forest have indicated that disturbances creating large openings and fire promote tree diversity only under low browsing pressure (Nuttle et al., 2013). Natural regeneration in spruce monocultures in conversion is especially vulnerable to browsing (Klimo et al., 2000; Diaci, 2002). Deer tend to concentrate in stands damaged by natural disturbances due to increased food and shelter resources (Widmer et al., 2004). This may slow down the development of forest succession since most pioneer species are highly palatable (Gill, 2006). In addition, pioneers are often rare in commercial forest due to the prevalence of small-scale management with low light levels. They are also extracted in the course of tending operations. Overbrowsing can also decrease the commercial value of future stands since it increases undesirable seedling growth patterns (multi-trunking, stem forking) and decay (Welch et al., 1991; Gill, 1992; Rea, 2011). On the other hand, faster growth of seedlings within large clearings and the abundance of other food resources may also positively influence forest succession.

Besides browsing, the distance to the forest edge and meso-relief are strong drivers of natural regeneration in larger openings. The forest edge often has a positive effect on regeneration density due to the proximity of seed trees and the positive influence of forest climate (Hanssen, 2003), with the exception of light-demanding species and sites with heavy root competition (Coomes and Grubb, 2000). Relief features such as sinkholes induce change in the overall soil and climatic conditions (Geiger et al., 2009) and may also be avoided by the herbivores. Given the rarity of studies addressing transformation of spruce monocultures affected by the interplay of acute and chronic disturbance, we established a field experiment after a large-scale European spruce bark beetle outbreak in the lowlands of the Dinaric region in southern Slovenia. We studied the effects of meso-relief, forest edge, seed trees and ungulate browsing on vegetation succession and tree regeneration. We hypothesised that locations within sinkholes with deeper soils as well as the proximity of the forest edge and seed trees would favour tree regeneration, while overbrowsing would result in lower regeneration coverage and density as well as decrease species diversity and thus delay succession and conversion.

2. Materials and methods

2.1. Stand and site characteristics

This study was carried out in the lowland spruce stands of the Vrbovec forest management unit (FMU) (45°41′10″N, 14°50′22″E) northeast of Kocevje in the Dinaric region of southern Slovenia. The parent material is composed of Upper Cretaceous rudist limestone with local deposits of silicate parent material. The terrain is flat but interwoven with numerous karst depressions and sinkholes. The soil type varies from rendzinic leptosol to podzolic calcocambisol (Anon., 1971a). The elevation of the research plots ranges from 460 to 475 m a.s.l. Mean annual precipitation at the nearby meteorological station in Kocevje (467 m a.s.l.; period 1960–90) amounted to 1523 mm, and mean annual temperature was 8.3 °C (Mekinda-Majaron, 1995).

In 1970 successional spruce stands in FMU Vrbovec covered 600 ha (Anon., 1971b). They established between 1880 and 1900 and were mostly the result of successional development of forest vegetation on agricultural lands that were abandoned following "The Long Depression". Continued agricultural overuse of lands caused soil degradation, which, in combination with seed sources from scattered older spruce plantations, influenced the prevalence of spruce in successional forests. However, artificial regeneration cannot be completely ruled out since some smaller parcels were sown and planted with spruce. The potential natural vegetation of the analysed stands is estimated as a transition between beech (*Fagus sylvatica* L.)-sessile oak (*Quercus petraea* (Matt.) Liebl.) forests and silver fir (*Abies alba* Mill.)-beech forests (Anon., 1971a). After WWII spruce stands were treated with thinning methods typical for Central Europe (Leibundgut, 1984). In 2010 the growing stock of the remaining stands amounted to 276 m^3 ha^{-1} and was comprised of spruce (72%), sessile and turkey oak (*Q. cerris* L.) (6%), noble broadleaves (6%), beech (4%), other broadleaves (2%), Scotch pine (*Pinus sylvestris* L.) (1%) and pioneer species (1%) (Anon., 2011).

In 2003 a heavy bark beetle infestation damaged large parts of the stands in the four forest compartments. The outbreak followed an extremely hot and dry year and a localised hailstorm and windthrow. In the same year damaged trees were salvaged and felling residues stacked in piles and burned. The size of openings amounted to 5.35, 5.63, 7.47 and 5.46 ha in compartments 37, 39, 42 and 51, respectively. In the following year compartments 37 and 39 were fenced to exclude browsing by roe and red deer. At the time of the study the estimated densities of roe (*Capreolus capreolus* L.) and red deer (*Cervus elaphus* L.) in the area were about 1 and 12 individuals per square kilometre, respectively (Adamic and Jerina, 2010; Nagel et al., 2015). The research area being red deer core habitat, these were among the highest regional densities in Slovenia. Planting was carried out in 2004 on small parts of the openings.

2.2. Sampling design and recordings

In autumn 2005 in the four openings, 240 research plots 1.5×1.5 m in size were installed in a randomly stratified manner. The openings were stratified according to three factors, each with two levels: fencing, meso-relief (karstic depressions or plateaus)