



Gap size and position influence variable response of *Fagus sylvatica* L. and *Abies alba* Mill.



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ABSTRACT

Montane forests of silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.) in the Dinaric region are the largest continuous forest area in Central Europe, where silver fir's regression is one of the region's major concerns. Designing appropriate sized canopy gap spatio-temporal dynamics is the main silvicultural tool for indirect promotion of silver fir. Within gap microsites, categories based on shares of direct and diffuse radiation proved to be an interesting conceptual model for explaining microsite variation and seedling success induced by light and general climate variability.

In order to evaluate the response of beech and fir in different gap microsites, different light regimes were evaluated based on the proportion between direct and diffuse radiation in three different sizes of forest gap in managed forests. The photosynthesis response to different light conditions (max. photosynthetic rate – A_{max} and quantum yield – Φ) in beech and silver fir was compared on all microsites during three consecutive g periods (2009, 2010, and 2011) under controlled environmental conditions.

A different response between species in microsite light categories was shown between different gap sizes. In all microsite categories of both species, quantum yield appeared at lower light intensities with increasing gap size, with the exception of beech with a predominant direct light component, in which yield significantly increased. In order to favour fir, gaps with low direct light levels should be created, while existing gaps should be extended towards the southern gap edge. Our conclusions emphasize the importance of gaps, relatively smaller in size (0.03–0.11 ha) but significant in contributing to increasing the competitive advantage of fir in mountainous, mixed-species Dinaric forests.

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1. Introduction

Montane forests of silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.) in the Dinaric region are the largest continuous forest area in Central Europe (Horvat et al., 1974). Most of these forests were gradually transformed from old-growth conditions and have never experienced clear cut silvicultural systems and extensive planting (Bončina, 2011; Bončina et al., 2014). From the onset of regular forestry, they were managed with continuous cover silvicultural systems; especially with selection systems, irregular shelterwood or their combination (Mlinšek, 1972; Bončina, 2011). It seems likely that these systems mimic some of the processes typical for natural disturbance regime of mixed old-growth forests in the region (e.g. Nagel and Diaci, 2006; Nagel et al., 2010; Motta et al., 2011).

These forests today harbour important protected areas (e.g., national parks, Natura 2000) and represent habitats for many

endemic and endangered species. In spite of the high degree of forest naturalness, silver fir (hereafter fir) regression is one of the major concerns for the whole region. It was already observed in the 1930s and 1950s and attributed mostly to climatic extremes coupled with bark beetle epidemics (e.g. Bambulović, 1930; Šafar, 1951). Polluted air later contributed to silver fir decline (Elling et al., 2009), while its regeneration was exposed to over-browsing in parts of the region (Mlinšek, 1969). Forest management activities, which induced changes in forest climate due to heavy felling or building of forest infrastructure, are also often cited as causes of silver fir regression (Mlinšek, 1964) but most of the evidence is questionable. The intensity of fir regression has varied due to different combinations of causes of decline across the region (Diaci et al., 2011), fir share in growing stock has even increased in some managed forests within the region (Bončina, 2011). However, current breast height diameter (dbh) structure and regeneration characteristics indicate further regression of fir in the coming decades (Bončina et al., 2009).

Silver fir has also suffered a similar fate elsewhere in Europe (e.g. Schütt, 1978; Krause et al., 1986; Heuze et al., 2005a). In

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addition to polluted air and overbrowsing, climate change is believed to have had an adverse impact on the growth performance of autochthonous fir populations in Europe in recent decades: Macías et al. (2006) found an increasing water-stress effect on radial growth of fir during the second half of the 20th century in the Pyrenees, while in the Mediterranean region, Battipaglia et al. (2009) showed that fir is more sensitive to drought and changes in the seasonal distribution of precipitation than non-native Norway spruce.

Conservation of silver fir is vital from ecological and economic perspectives. It is a large tree important for site productivity and it forms many special habitats as a veteran or slowly decomposing dead tree. It is economically valuable and, within the Dinaric region, the most important conifer. While causes of fir decline such as climate change, air pollution and overbrowsing are difficult to control, factors that could be effectively influenced by silvicultural measures (e.g., creation of suitable stand climate, promotion with tending and preservation of seed trees) are becoming even more significant for its conservation.

Fir and beech, as the main coexisting species in mountainous, mixed-species forests, are shade tolerant, and can thrive under conditions of deep shade for extended time periods (Ellenberg, 1988). Fir is a late successional tree, more sensitive to water deficits than beech (Rolland et al., 1999) on drier sites and in periods when generating stocks for the next growing season (Macías et al., 2006). Its photosynthetic activity is not limited only to the vegetation period, such as in beech, and it can assimilate over the entire year (Brinar, 1964). Needles are sensitive to temperature oscillations and rapid changes, especially at the beginning of the vegetation period and in combination with drought (Prpić and Seletković, 2001). The specific assimilation capacity of fir is lower; the lower pigment rate in leaves reflects its greater shade tolerance and ability to grow assimilation tissues under lower light intensities than beech. Costs for establishing leaves are not seasonally conditioned as in beech, the needle cuticle is thicker and assimilation losses are smaller (Aerts, 1995). Its competitive strength, compared to beech, is consequently less; in gap-openings, beech adapts better and much faster to rapid changes in light intensity (Lichtenthaler et al., 2007).

The main silvicultural tool for indirect promotion of silver fir is the creation of appropriate sized canopy gaps and their extension in time and space. While there have been many studies that have indicated fir's supremacy under relatively closed canopies (e.g. Hohenadl, 1981; Stancioiu and O'Hara, 2006; Nagel et al., 2010), most of them have focused on different growth patterns and did not consider the ecophysiological processes involved. Moreover, the findings are difficult to transfer into practice since most research did not account for the gap spatio-temporal dynamics and heterogeneity in light regimes (*sensu* Poulson and Platt, 1989; Canham et al., 1990). Dividing into four categories within gap microsites based on the shares of direct and diffuse radiation proved to be an interesting conceptual model for explanation of microsite variation and seedling success induced by light and general climate variability (e.g. Diaci, 2002; Diaci et al., 2008). Moreover, this simple division also indicates a distribution of other ecological factors. For example, direct radiation is associated with increased evapotranspiration, which may imply higher drought probability, diffuse radiation indicates the rainfall pattern within gaps (Krecmer, 1967) and thus accelerated humus decomposition rates, as well as reduced competition in the rhizosphere (Diaci et al., 2000).

The main goals of this study were the following: (1) to analyse whether young beech and fir trees growing in four different microsite categories based on light asymmetry within gaps show different acclimatisation to light, (2) to analyse which of the microsites are more favourable for each of the two species and

(3) to discuss appropriate silvicultural systems to help conserve the fir population in the Dinaric mountains.

2. Methods

The research was performed in the Kočevski Rog high karst Dinaric forest complex, located in the southwestern part of Slovenia (Fig. 1).

2.1. Site conditions

All research sites belong to the Dinaric silver fir and beech forest type *Omphalodo-Fagetum* with homogenous Rendzic Leptosol (Kutnar and Urbančič, 2008), higher than 720 m above sea level (Table 1).

Three gaps, differing in size, were selected on flat terrain in managed forests, in which both species were found growing in all light categories. All selected gaps had been established at least 10 years ago, so young beech and fir had been able to adapt to the given light conditions.

2.2. Microsites

A systematic grid was established in each gap and four distinctive light microsites within a gap were defined (A, B, C and D) with hemispherical photos according to the relative abundance of direct and diffuse light (Diaci, 2002) (Fig. 2).

The relative percentages of diffuse (FDIF) and direct radiation (FDIR) were estimated from digital hemispherical photographs taken in completely overcast sky conditions at 1.3 m height with a DSLR Canon EOS Rebel T3i digital camera and calibrated fish-eye lens from Regent WinScanopy accessories prior to all measurements. Light intensity parameters were processed with WinScanopy pro-d software (Čater et al., 2013). The height difference of trees of the same age on plots ranged from 15 to 30 cm under dense stand conditions, from 25 to 70 cm under edge conditions (light microsites C and D) and from 65 to 200 cm in open area conditions (light microsites A and B) (Čater and Levanič, 2013). On each microsite (A, B, C, D), at least eight each young beech and fir trees of the same height, unobstructed by their neighbours, were randomly chosen for photosynthesis measurements, which were performed in three sequential vegetation periods (2009, 2010 and 2011).

In the same leaves nitrogen concentration (mg/cm^2) was determined to compare macronutrient status (Leco CNS-2000 analyser). Water use efficiency of photosynthesis (WUE) was expressed as the ratio of carbon gain per water lost ($\text{mol H}_2\text{O}/\mu\text{mol CO}_2$) (Larcher, 1995), while photosynthetic nitrogen-use efficiency (PNUE) was expressed as carbon gain per unit of leaf nitrogen ($\mu\text{mol CO}_2/\text{gN}$) (Lambers et al., 1998) for each light category. A total of 20 leaves was sampled per tree in the upper crown position, then cool-stored in airtight conditions. Fresh leaves were weighed and scanned for leaf area. Leaves were dried at 105°C

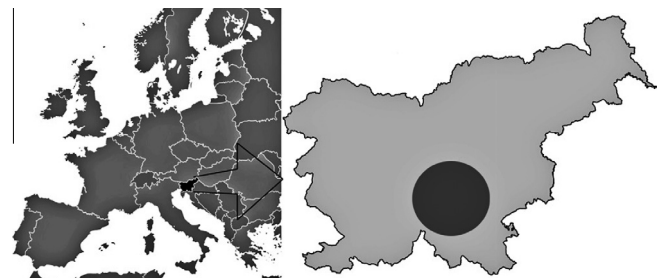


Fig. 1. Study area of Kočevski Rog in Dinaric karst, Slovenia.

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