

Light response of *Fagus sylvatica* L. and *Abies alba* Mill. in different categories of forest edge - vertical abundance in two silvicultural systems

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Abstract

In managed Dinaric montane fir (Abies alba Mill.) and European beech (Fagus sylvatica L.) forests, the light response of young beech and fir in gap microsites was studied during three consecutive growing periods (2009, 2010, and 2011) under controlled environmental conditions in stands of single-tree and irregular shelterwood silvicultural system. According to maximal quantum yield, the different response between species in microsite light categories was evidenced for silver fir on microsites with predominating diffuse light and for beech on microsites with predominating direct light, respectively. Abundance and change of share in microsite light categories was compared over different elevation belts on comparable sites between two silvicultural systems. The share of forest edge area was bigger in the irregular shelterwood system. Change in width of forest edge (20, 30 and 40 m) did not affect the proportion and share of the microsite in both regions of different silvicultural system. Separation of microsite areas between both silvicultural systems, evident in lower elevation belts was not evident in the most conflict and highest elevation zone, while the absolute values of all categories above 700 m in both systems were almost identical, indicating the same, small-scale irregular shelterwood system, known also as the freestyle silvicultural approach.

Keywords

Fagus sylvatica, Abies alba, Dinaric silver fir and beech forests, forest edge, silviculture, selective system, irregular shelterwood system

1. Introduction

Montane forests of silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.) in the Dinaric region represent the largest contiguous forest area in Central Europe (Horvat et al., 1974), characterized with continuous cover silvicultural systems. In particular, selection and irregular shelterwood systems predominate (Mlinšek, 1972), which are close to the natural disturbance regime of mixed old-growth forests and characterized by small to intermediate gap size dynamics (Motta et al., 2011).

Most of Dinaric beech and fir forests were gradually transformed from old-growth conditions and have never experienced clear-cutting or extensive planting (Bončina, 2011; Bončina et al., 2014). They were managed with continuous-cover silvicultural systems; especially with single-tree selection systems, irregular shelterwood or their combination (Schädelin, 1928; Leibundgut 1946; Mlinšek, 1972; Bončina, 2011). The *selection system* (Schütz, 2001) developed as the main alternative to the clear-cutting system with long tradition in Slovenia, Switzerland, and France is characterized by trees of different sizes (height and diameter at breast height (dbh)) and ages growing together in areas smaller than 0.1 ha. If trees are grouped in larger cohorts, we talk of *irregular shelterwood systems* (Matthews, 1999; Raymond et al., 2009). Patch sizes vary from a few hundred square meters to a few hectares, with often indistinctive edges and dynamic horizontal structure, because of silvicultural measures, tree growth, regeneration and natural disturbances.

Beech and silver fir (hereafter fir) forests grow best in altitudes between 600 and 1200m above sea where submediterranean, atlantic and continental climate regions ensure sufficient humidity and water availability (Rubner, 1953). During last decades, much attention was dedicated into firs decline (Elling et al., 2009) and difficulties with natural regeneration because of severe deer browsing (Ammer, 1996; Motta, 1996; Heuze et al., 2005a, 2005b). Today's situation is accompanied by the decline of abundance

especially in the Dinaric silver fir and beech forests (Poljanec et al., 2010). Almost 50% of living stock is accumulated in trees with dbh bigger than 50cm with small or no recruitment. Situation is worsened by high browsing rate as well as evidenced smallest share of fir saplings in the regeneration, particularly in elevations above 700m asl (Battipaglia et al., 2009, Chaucard et al., 2010).

Fir and beech are shade tolerant, and could thrive under conditions of deep shade for longer time periods (Ellenberg, 1988). Fir is late successional tree, more sensible to water deficits than beech (Rolland et al., 1999) on drier sites (Macias et al., 2006). Its photosynthetic activity is not limited only to the vegetation period, such as in beech and could assimilate over a whole year-period (Brinar, 1964). Needles are sensitive to temperature oscillations and rapid changes, especially at the beginning of the growing season and in combination with drought (Prpić and Seletković, 2001). Specific assimilation capacity of fir is smaller; lower pigment rate in leaves reflects its bigger shade tolerance and ability to grow foliage under lower light intensities than beech. Costs for establishing leaves are not seasonally conditioned as in beech (Aerts, 1995). Its competitive strength compared to beech is smaller; in gap-openings beech adapts better and much faster to rapid changes in light intensity (Lichtenthaler et al., 2007).

Main silvicultural tool for indirect promotion of silver fir is creation of appropriate sized canopy gaps and their extension in time and space. Most of studies indicated fir's supremacy under relatively closed canopies (e.g. Hohenadl, 1981; Stancioiu and O'Hara, 2006) and focused on different growth patterns without consideration of ecophysiological processes involved. Findings are also difficult to transfer into practice since most research did not account for the gap spatiotemporal dynamics and heterogeneity in light regimes (Canham et al., 1990). Dividing gap microsites according to shares of direct and diffuse radiation into four categories 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), where species compete for light. Microsite position significantly influenced the quantum yield (Φ) (Lambers et al., 1998) of young beech and firs, which changed with gap size, explaining their difference in competitive ability (Čater et al., 2014). Such division may also be associated with spatial distribution of other ecological factors: direct radiation may be connected with an increased evapotranspiration and higher drought probability, while diffuse radiation with rainfall patterns within gaps (Kremer, 1967).

The quality and proportion of present and future fir-beech forests is in tight connection with our understanding of tree-response to different light conditions. Light as a predominating environmental factor controls the relationship between seedling development and weeds and also exerts an influence on tree species diversity, thus controlling the tree species mixture relationship (Schütz, 2004). Understorey trees recruit to the upperstorey when light conditions are favourable (Schütz, 2001). Fir's competitive strength is compared to beech consequently smaller; in openings and gaps beech adapts better and much faster to rapid changes in light intensity (Lichtenthaler et al., 2007).

Our study was oriented toward evaluation of light response in beech and silver fir in different light categories found at forest edge conditions, where both species compete for light and exhibit different competitive strategies (1). As the structure between selection and irregular shelterwood system varies, it was our intention to evaluate differences of light microsite abundance in both areas of predominating single tree and irregular shelterwood system. Abundance of pre-determined light categories was compared over different altitudes (e.g altitude gradient) on comparable sites in both silvicultural systems (2). Emphasis was given to the elevations above 700 m, where most regeneration problems with silver fir were identified. Situation from both systems was also compared with old growth reserve in corresponding elevation belt (3).

2. Material and methods

2.1 Study area and the experiment design

The research was performed in Kočevski Rog, a high karst Dinaric complex located in the south-western part of Slovenia (Fig. 1). Beech and fir assimilation was compared between different microsites with single tree-selection system (S) and sites with applied irregular shelterwood system (I) in same light categories (Čater and Levanič, 2013). The research area covers 35392 ha in total, including 13188 ha (37.3%) of the predominating single-tree selection silvicultural system (S) with 91.1% forest cover and 22203 ha (62.7%) of the irregular shelterwood system (I) with 87.3% forest cover, respectively (Fig. 1, Table 1).



Figure 1: Location of the research area: S - the part with predominating single tree-selection system and I - the part with the irregular shelterwood system; forested area (right) is grey.

Table 1: Research plots

Plots	Elevation (m)	Latitude (°)	Longitude (°)	Annual precipitation (mm)	Annual Average air T (°C)	Growing stock (m ³ /ha)
Single tree selection (S)	350-835	45°42'44''	14°56'30''	1520	6.5	482
Irregular shelterwood (I)	350-750	45°36'37''	15°05'33''	1485	7.2	490
Old growth	790-860	45°39'36''	15°03'36''	1530	6.2	992

The studied sites belong to the Dinaric silver fir and beech forest type *Omphalodo-Fagetum* (Kutnar and Urbančič, 2008), characterized by low average temperature (6-8°C), large amount of precipitation (1500-2500 mm), south-east to north-west orientation of mountain ridges and valleys and carbonate substrate, which consists mainly of limestone and partly of dolomite with cambisols and leptosols of different depths (Bončina, 2011).

In the first part of the experiment the quantum yield (Φ) of fir and beech was measured within gaps in four different light microsites, according to the share of direct and diffuse light (Čater et al. 2014). At the same time, foliar nitrogen, water use-efficiency and photosynthetic-use-efficiency were defined for both species in all microsites. Light conditions, most favourable for beech and for fir were defined for regions of both silvicultural systems.

In the second part the same four microsite-categories were defined for every segment of the forest edge: not only in forest gaps but along all forested border within both management systems and old growth reserve, regarding the orientation and position of forested area and openings. Share of every microsite was then compared between both silvicultural systems within 100m elevation bands for different width of forest edge - 20m, 30m and 40m.

2.2 Microsite light categories

At first, twelve gaps along both test sites (S and I) and altitudes were selected at random, six in each silvicultural system, from 370m² - 450m² in size. In each gap a systematic grid with 4 x 4m resolution was established for the evaluation of potential light with hemispherical photos, from 25-40 photos per gap, depending on the shape and the size of the gap. Four distinctive light microsites (A, B, C and D) in each gap were defined according to the relative percentages of potential diffuse (*diff*) and direct radiation (*Dir*) (Diaci, 2002; Čater et al., 2014), estimated from digital hemispherical photographs. Photos were 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 for every microsite were processed with WinScanopy pro 2013a software (Čater et al., 2013). Distribution of microsite gap categories in field (Fig. 2, left) and in perfectly circle-shaped gap (Fig. 2, right) are presented.

Age of studied trees (10-15 years) was determined by the number of tree rings 10 cm above the root collar using stereo-microscope. The height difference of trees of the same age on studied plots ranged between 25-70 cm in light microsites A, C and D, and between 65-200 cm in the open area conditions (microsite B) (Čater and Levanič, 2013; Čater et al., 2014).

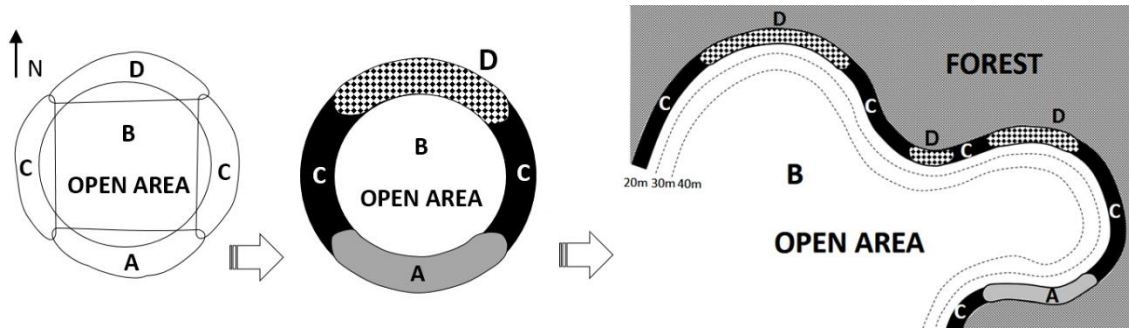


Figure 2: Microsite light categories according to potential diffuse (*diff*) and direct (*Dir*) radiation in a regular, round shaped gap (A - high *diff* and low *Dir*; B - high *diff* and high *Dir*; C - low *diff* and low *Dir*, and D - low *diff* and high *Dir*) (middle) simplified shape for further spatial analysis (right) and their position on an actual forest edge (right). Part (B) corresponds to the microsite without mature canopy cover, while categories A, C and D to microsities at the forest edge, under fragmented canopy cover (Čater et al., 2014).

2.3 Quantum yield

The assimilation yield of beech and silver fir was measured in twelve gaps, randomly distributed along both test sites (S and I) and altitudes. On each microsite category (A, B, C, D) at least eight young beech and fir trees of the same height, unobstructed by their neighbours were randomly chosen for light saturation measurements, performed during three sequential growing seasons (2009, 2010 and 2011) (Čater et al., 2014). The light-response was measured with an LI-6400 portable system on at least four sun leaves/locations per tree, located in the upper third of the tree-crown.

Light saturation curves were established to compare the net assimilation (AS_{max}) in young beech and fir to different microsities under comparable light conditions. All assimilation measurements were performed in field at a constant temperature of the measurement block ($20^{\circ}C$), a CO_2 concentration of $400 \mu mol/l$, flow $500 \mu mol/s$ and different light intensities: 0, 50, 250, 600 and $1500 \mu mol/m^2s$. Maximum assimilation (AS_{max}) rates for the light saturation curves were used for comparisons of responses between different microsities.

A-Ci curves were established to compare and define assimilation response of trees (AS_{max}) to different intercellular CO_2 concentrations (C_i) at constant light $1200 \mu mol/m^2s$, while ambient CO_2 was varied as 0, 50, 100, 350, 700 and $1000 \mu mol/l$. All assimilation values were recorded after they had held constant until the coefficient of variability (CV %) dropped below 5%. The characteristic points of maximal quantum yield (Φ_{max}), defined as the maximal amount of fixed CO_2 per amount of absorbed light quanta (Lambers et al. 1998) were defined for each light microsite and both species, as described in Čater et al. (2014) (Fig. 3).

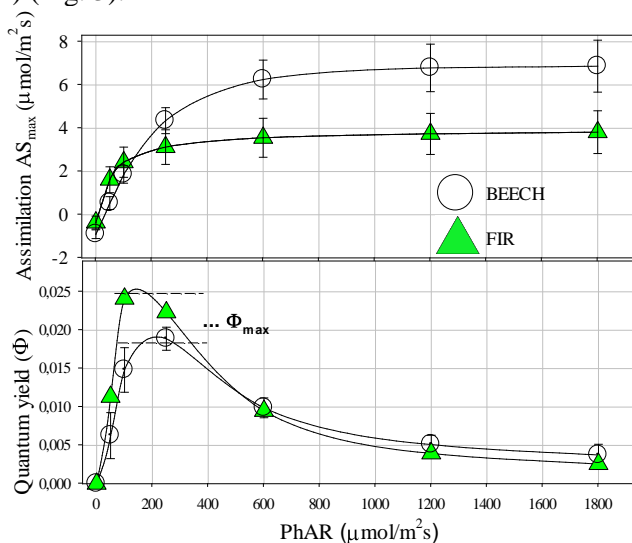


Figure 3: Beech and silver fir light responses on microsite B for the small gap size ($370m^2 - 450m^2$): from the light saturation curves (top) a quantum yield Φ curves (bottom) were derived. Light intensity change was compared at the point where both species expressed their maximum (Φ_{max}). Same curves were established for both species and microsite category (Čater et al. 2014).

Nitrogen concentration (mg/cm) 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 [$\mu\text{mol CO}_2/\text{mol H}_2\text{O}$] (Larcher, 1995; Lambers et al., 1998), while photosynthetic nitrogen-use efficiency (PNUE) as the carbon gain per unit leaf nitrogen [$\mu\text{mol CO}_2/\text{gN sec}^{-1}\text{m}^{-2}$] (Larcher, 1995; Lambers et al., 1998) for forest edge (A, C, D), open area (B) and category under shelter of mature trees (Čater and Simončič, 2009). A total of 20 leaves were sampled per tree in the upper crown position, then cool-stored in airtight conditions. Fresh leaves were weighed and scanned for the leaf area. Leaves were dried at 105° for 24 hours until constant weight and weighed for the dry mass in the lab.

2.3 Spatial analysis

The spatial analysis resulted in identification and measurement of the area in the zones, belonging to different microsite light categories along the forest border within the forest clearings. The light conditions were determined in terms of relationship between the direct (*Dir*) and the diffuse (*diff*) component of solar radiation (Fig. 2). Identification of zones, belonging to different microsite light categories has been performed according to the following procedure:

1. The forest border was derived from the vector GIS-layer of the Agricultural Land Use Map (ALUM) of Slovenia, 1:5.000 scale, map publication date March 31, 2015. The »Forest« class (class ID = 2000) of the ALUM map was considered as the forest and all other classes as the non-forest. The border between the two groups of classes was considered forest border, the resulting binary map was rasterized with 1 m spatial resolution.
2. The resulting raster map contained many false forest borders along narrow corridors due to forest roads, where forest canopy re-established from the both sides of the road. These corridors had to be removed from the map without removing the relevant corridors, belonging to public roads. To remove the non-relevant corridors from the binary rasterized map a morphological filter was used. Specifically, the morphological closing was used, where a morphological dilation using a structuring element with a diameter of 20 m was followed by a morphological erosion using the same structuring element. All public road corridors that were unintentionally removed - filtered out from the raster binary map (for being less than 20 m wide) were restored into the map, using vector GIS layer of public roads. The narrow corridor situation before and after removal is illustrated in Fig. 4.

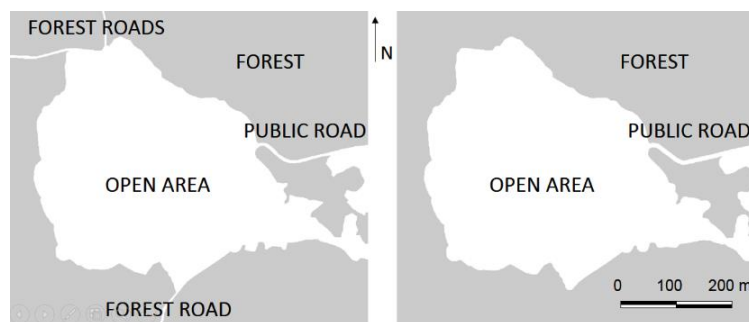


Figure 4: Illustration of the morphological filtering - removal of forest roads area from the forest map. The original map (left) and the filtered map (right).

3. A raster GIS tool for computing relief aspect (i.e., the azimuth of the relief exposition) was used to identify automatically the aspect of each segment of the forest border line, in our case the IDRISI GIS module ASPECT. To use the relief aspect GIS tool, first a relief “valley” was simulated, sloping down from the forest border towards the centre of each forest gap (Fig 5, top, left). This step was done using the distance raster GIS tool (IDRISI DISTANCE), assigning each pixel in the forest gap the value, corresponding to the pixel’s distance to the nearest forest border segment. These values were subsequently multiplied by -1 in order to get increasingly lower values for the pixels that are further away from the forest border. The negative distance values were considered as elevations, creating the desired “valley” relief topology (Fig 5, top, right). Using the simulated relief, the aspect along each segment of the forest border line was finally calculated, using the appropriate raster GIS tool (IDRISI ASPECT). The areas were intersected with the buffer areas of 20 m, 30 m and 40 m, respectively from the forest border towards the

clearing. The procedure of simulating a “valley” in the process of evaluating the forest border aspect is illustrated in Fig. 5.

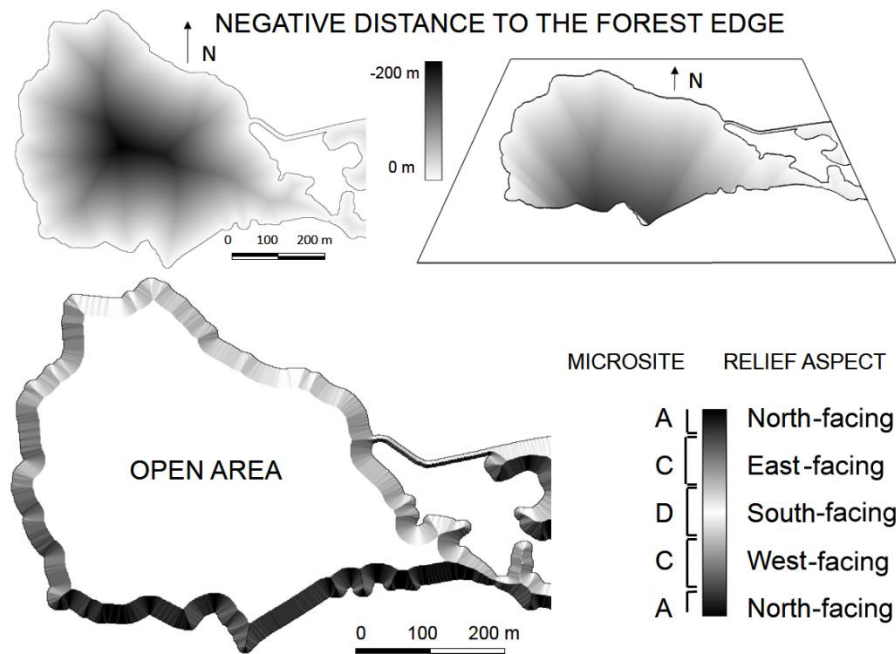


Figure 5: Detailed illustration of the forest border line identifying each segment: the negative distance image used as a simulated relief, i.e., the simulated “valley” (top left); the 3-D rendering of the simulated “valley” (top right) and the forest border aspect image, calculated from the simulated relief image, within a buffer from the forest border towards the clearing (bottom).

4. The areas of the forest edge were calculated separately for different widths of 20 m, 30 m, and 40 m, respectively, and separately for each 100-meter elevation belt with 12.5 m DEM. The terrain elevations were gleaned from the national Digital Elevation Model (DEM) in 12.5 m resolution (SMA 2006). A relatively coarse DEM (12.5 m horizontal resolution compared to 1 m resolution forest map) was not judged to be the analysis weakness, as the average relief slope within the forest edge areas is 8.8° (99% of the edge area is below 24°), and the elevations were only considered in broad 100 m classes.
5. Finally, the forest border aspect images (i.e. azimuth values of the aspect map) were reclassified into microsite light categories A, C, and D, respectively, according to the following aspect thresholds: aspects NE-SE = category C, SE-SW = category D, SW-NW = category C and NW-NE = category A (Fig. 5, bottom). Three different buffer widths (20 m, 30 m, 40 m) from the forest border towards the open area were taken into account when comparing the microsite light zones between the two silvicultural systems.

Shares of light microsities were compared between managed forests and old growth reserve, but only in the highest elevation belt (iii). Different shares of microsities would indicate different structure and orientation of forest gaps between two systems and consequently different light conditions for beech and fir. Both areas of single tree-selection system (S) and applied irregular shelterwood system (I) represent separate forest management areas that were evaluated as a whole. Our focus was in particular in the elevation belts above 700 m because of reported unfavourable regeneration conditions worsened by the higher presence of ungulates than in lower elevation zones.

2.4 Data processing

Differences in physiological response as well as shares between both silvicultural systems were evaluated with analyses of variance (ANOVA) after normality test and variance homogeneity; with post hoc LSD analysis the differences between microsite categories and different elevation belts were determined. Probability values of $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***) were considered significant. All data was analysed with the Statistica software system (2011).

3. Results

The leaf nitrogen amount for beech and fir was highest at the microsities B and lowest under shelter conditions on every plot. Differences between edge categories (A, C and D) and open area conditions were not significantly different on managed sites and old growth forest ($p \leq 0.715$, NS). The values for water use-efficiency (WUE) in beech were highest under shelter on all plots, ranging from 17.9-20.9 mol H₂O/ μ mol CO₂. At old growth, the maximum values were measured at the forest edge (20.9 mol H₂O/ μ mol CO₂) (Table 2).

Table 2: Average leaf nitrogen content per leaf area, water use efficiency (WUE) and photosynthetic nitrogen use efficiency (PNUE) in different light microsities (Shelter, A, B, C and D) and silvicultural systems for beech and fir (means \pm SE, n=36)

	Nitrogen (Ntot) [mg/g]			WUE [μ mol CO ₂ /mol H ₂ O]			PNUE [μ mol CO ₂ /gN sec ⁻¹ m ⁻²]		
	Shelter	A, C, D	B	Shelter	A, C, D	B	Shelter	A, C, D	B
Beech / microsities									
Single tree selection	21.7 \pm 0.8	22.3 \pm 0.7	23.3 \pm 1.6	19.9 \pm 3.3	18.8 \pm 3.2	15.2 \pm 1.9	0.10 \pm 0.006	0.08 \pm 0.002	0.08 \pm 0.003
Group selection	21.9 \pm 0.9	22.6 \pm 1.5	23.8 \pm 2.0	17.9 \pm 1.8	12.2 \pm 2.7	8.9 \pm 1.8	0.06 \pm 0.008	0.06 \pm 0.003	0.04 \pm 0.005
Old growth	20.9 \pm 0.8	22.4 \pm 0.6	22.9 \pm 1.3	20.3 \pm 2.6	20.9 \pm 3.1	19.9 \pm 3.3	0.08 \pm 0.006	0.06 \pm 0.002	0.05 \pm 0.006
Fir / microsities									
Single tree selection	14.1 \pm 0.2	14.5 \pm 0.4	14.9 \pm 1.2	13.4 \pm 2.1	11.7 \pm 1.9	10.2 \pm 1.4	0.09 \pm 0.005	0.07 \pm 0.002	0.06 \pm 0.002
Group selection	14.2 \pm 0.6	14.9 \pm 0.7	15.2 \pm 1.0	12.6 \pm 1.5	12.2 \pm 1.4	9.3 \pm 1.1	0.05 \pm 0.002	0.06 \pm 0.001	0.02 \pm 0.002
Old growth	14.2 \pm 0.7	14.4 \pm 0.5	14.9 \pm 1.1	13.5 \pm 1.7	13.0 \pm 2.1	10.9 \pm 1.3	0.08 \pm 0.005	0.06 \pm 0.002	0.04 \pm 0.003

Although the value measured at the forest edge (microsites A, C and D) in old growth sites was greater from that measured in open it was statistically not significant (20.9 mol H₂O/ μ mol CO₂ compared to 20.3 mol H₂O/ μ mol CO₂, respectively). A similar relation was determined for photosynthetic nitrogen use efficiency (PNUE), highest under shelter at single tree selection sites (0.10 μ mol CO₂/gN). Both fir and beech nitrogen content was within optimal threshold values (Grassi and Bagnaresi, 2001; Mellert and Göttelein, 2012).

3.1 Beech and fir's quantum yield in different forest gap microsities

Significant differences were confirmed between microsities, especially those with predominating direct light component. Quantum yield varied in different sizes of gaps according to different light intensity and by its absolute value. Light utilization was highest for silver fir under predominating diffuse light (microsites A and C), while for the beech under predominating direct light (microsites B and D) (Fig. 6). No significant differences between years within same microsite categories were observed.

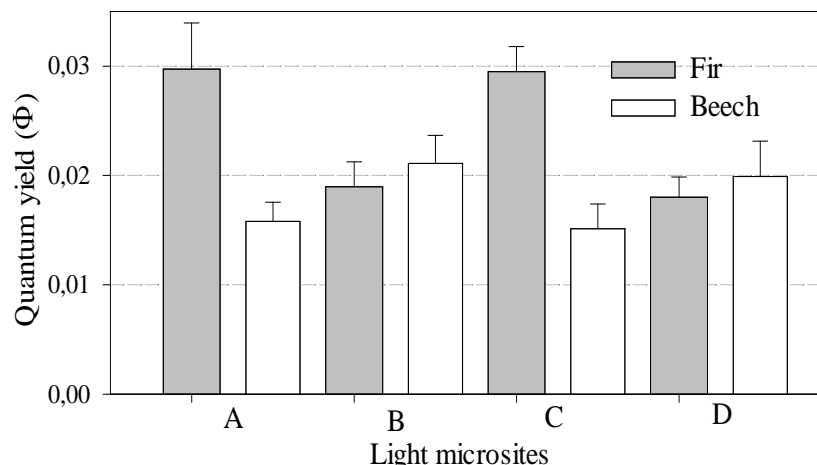


Figure 6: Average quantum yield in beech and silver fir in light microsite conditions. Bars are standard errors.

Differences in yield were evaluated and pronounced between microsities with predominating direct (B, D) and diffuse (A, C) light conditions (Table 3).

Table 3: Left: Significant differences in quantum yield (Φ) between microsite categories; shaded cells characterise relations for silver fir and non-shaded for beech. Right: Differences in Φ between beech and silver fir within

same light microsites. Probability values of $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***) were considered significant ($N_{\text{fir}}=196$, $N_{\text{beech}}=224$)

Microsite	A	B	C	D	Microsite	Beech - Silver fir
A	/	0,000***	0,542 NS	0,000***	A	0,000***
B	0.000***	/	0.000***	0.014 *	B	0.323 NS
C	0.384 NS	0.000***	/	0.000***	C	0.000 ***
D	0.000***	0.216 NS	0.001 **	/	D	0.014 *

Observed A-Ci response for beech and fir was found different between the species and without any differences between silvicultural systems and / or old growth forest reserve (Fig. 7).

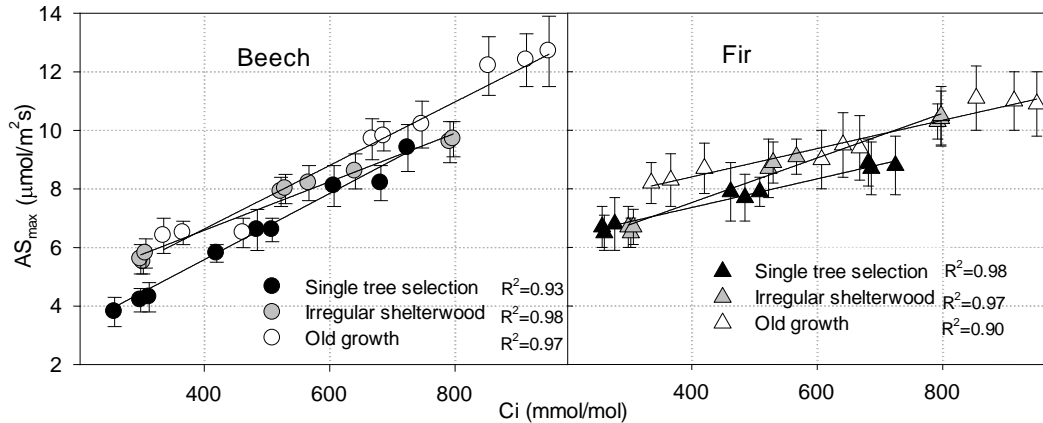


Figure 7: Beech (left) and fir (right) response on studied sites to different intercellular CO₂ (Ci). Significant differences in slopes were observed between species on all sites ($p < 0.01$).

As microsites B represent the open-area light conditions without shelter, caused by the mature canopy stand, only the microsites A, C and D (Fig. 2), which are directly in the forest edge conditions were used for the further analysis.

3.2 Forest edge area of microsites in different bandwidth and altitude

Observed microsite categories and their abundance was presented in 100-meter elevation bands. The microsite abundance for different elevation belts is presented in the table 4.

Table 4: Corresponding share of microsite categories (in %) for irregular shelterwood system (I) and single tree selection system (S) in different elevation belts. Probability values of $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***) were considered significant.

Elevation belt	Irregular shelterwood (I)				Single tree selection (S)			
	A	C	D	Total	A	C	D	Total
100 - 199 m	0.53	4.66	4.76	9.95	0.01	0.01	0.01	0.03
200 - 299 m	1.95	10.25	7.62	19.81	0.28	1.84	0.71	2.83
300 - 399 m	2.42	13.11	9.27	24.80	2.89	8.59	5.69	17.17
400 - 499 m	2.06	10.73	7.54	20.32	2.87	10.98	6.92	20.77
500 - 599m	0.87	4.13	2.82	7.82	1.98	9.98	8.67	20.63
600 - 699 m	0.83	3.76	2.68	7.28	3.63	13.54	7.97	25.14
700 - 799 m	0.44	2.18	1.64	4.26	0.65	4.57	1.19	6.41
800 - 899 m	0.40	2.45	1.47	4.32	0.39	3.25	1.30	4.94
900 - 999 m	0.10	0.76	0.55	1.41	0.22	0.98	0.73	1.93
1000 - 1100 m	0.01	0.02	0.01	0.02	0.01	0.12	0.05	0.19
Total	9.61	52.05	33.41	100.00	12.93	53.85	33.23	100.00

Shares refer to the total area of forest edge category within studied silvicultural system (S and I). No significant difference between different bandwidths of 20 m, 30 m or 40 m defined strip of the forest edge were confirmed - shares of the observed light microsites were the same. Most of the fragmented area was located within single tree selection system in altitudes between 300-699 m and in the elevation belt between 100-499 m in the irregular shelterwood system. Smallest share of forest edge area in both systems was found in the highest elevation belt. With increasing altitude (above 700m) shares of forest edge and consequently shares of microsites became equal. Change of band width did not affect the

proportion of the microsite categories in both studied parts (S and I) of different silvicultural systems (Fig. 8).

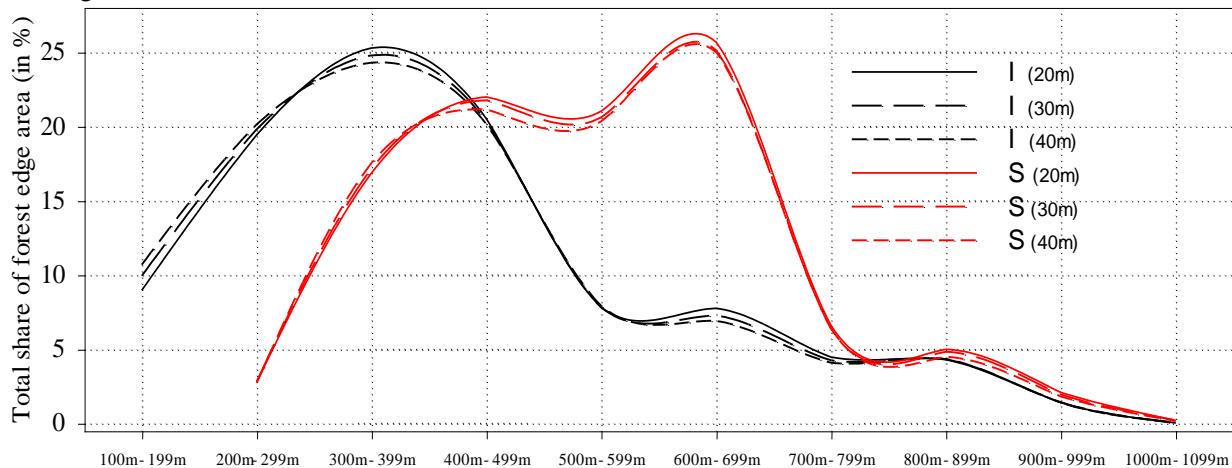


Figure 8: Distribution of forest edge area in irregular shelterwood (I) and single tree selection system (S) along 100m elevation belts. Various bandwidths (20m, 30m and 40m) of forest edge are presented.

The abundance of microsite A (corresponding to south-oriented parts of forest edge) with least direct and most diffuse light was in both systems the smallest. Highest was the share of microsite C with low proportion of both direct and diffuse light component (east and west-oriented parts of the forest edge), while the abundance of microsite D (northern exposures) was found in-between of both microsite categories. In total, share of microsities A and C in the single selection silvicultural system was slightly higher (12.9% and 53.9%, respectively), compared to the irregular shelterwood system (9.6% and 52.1%, respectively).

Shares of different microsities were statistically different within both silvicultural systems and between elevation belts within each microsite (Table 5).

Table 5: Differences between shares of microsities in silvicultural systems (left) and between elevation belts and same microsite within silvicultural system (S-single tree selection system; I-irregular shelterwood system) (right). Probability values of $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***) were considered significant.

Microsite	S	I	Microsite	S	I
A-C	0.000***	0.000***	A	0.000***	0.000***
A-D	0.000***	0.000***	C	0.000***	0.000***
C-D	0.000***	0.000***	D	0.000***	0.000***

Separation of microsite areas between both silvicultural systems, evident in lower elevation belts was not observed in the highest altitude zone. Shares of microsite categories above 700m in both systems were almost identical, in all three microsities (Table 6 and 7).

Table 6: Post-hoc analysis between silvicultural systems (S and I) and microsite shares (A, C and D) in elevation belts. Probability values of $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***) were considered significant.

Elevation belt	S - I difference		
	A	C	D
100 m - 199 m	0,0000***	0,0000***	0,0000***
200 m - 299 m	0,0000***	0,0000***	0,0000***
300 m - 399 m	0,0000***	0,0000***	0,0000***
400 m - 499 m	0,0001***	0,0174*	0,0095**
500 m - 599 m	0,0000***	0,0000***	0,0000***
600 m - 699 m	0,0000***	0,0000***	0,0000***
700 m - 799 m	0,1119 NS	0,0312*	0,0298*
800 m - 899 m	0,3247 NS	0,0473*	0,0589 NS
900 m - 999 m	0,1926 NS	0,0507 NS	0,1345 NS
1000 m - 1100 m	0,9881 NS	0,0978 NS	0,0894 NS

Table 7: Microsite categories (in %) in four highest elevation belts of both managed single tree selection system (S), irregular shelterwood system (I) and old growth (O). Almost identical share of all three microsites were observed regardless to width of forest edge.

Microsite (%)	20-m band width			30-m band width			40-m band width		
	S	I	O	S	I	O	S	I	O
A	10.91	9.50	12.41	11.09	9.48	12.83	11.27	9.47	12.92
C	54.15	53.91	57.23	54.26	54.00	57.76	54.27	54.07	57.94
D	34.95	36.59	30.36	34.65	36.52	29.41	34.46	36.46	29.14
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

4. Discussion

4.1 Response of beech and fir to microsite light categories

The behaviour of beech and fir is influenced by the general shade tolerance mechanisms and ability to outcompete their neighbours in conditions of favourable light. Both species may be influenced by careful overstorey selection or a fine adjustment of light permeability and improving conditions for growth and development in reintroduction practices. Different quantum yield between studied species in all conditions of forest edge emphasizes the importance of marginal light conditions, where shading and light conditions are directly affected by the mature overstorey.

Light utilization efficiency (quantum yield) proved in our case significantly different between studied species, showing fir's advantage in diffuse light conditions (microsites A and C) over beech, which predominates in direct light conditions (microsites B and D) not only within a single elevation category (Čater et al. 2014), but also on a wider spatial scale and altitudes. Total shares of diffuse light microsites in single tree selection system were also higher than in irregular shelterwood system, supporting our former research (Čater and Levanič, 2013), with firs lower compensation point and also better shade tolerance in single tree selection system.

Fir may display physiological and morphological plasticity to contrasting light levels, but over longer time periods than beech (Robakowski et al., 2004). Its adjustment of growth rate to the light environment occurs gradually over several years (Robakowski et al., 2004) and can be seriously compromised by competition with young beeches, which perform more vigorously at a young age (Szewczyk and Szwagrzyk, 2010). Beech, a less sensitive species to competition, still displays relatively high basal area growth when experiencing moderate competition levels (Szwagrzyk et al., 2012), while fir reacts to the intensity of competition much more strongly (Szwagrzyk and Szewczyk, 2001). As a tall tree, silver fir can reach the upper canopy and often grows as an emergent species (Korpel, 1995; Paluch, 2007), relatively free of competition from other species for light. Beech on the other hand utilizes direct light more efficiently and over competes fir in the middle of gaps (microsite B), as demonstrated in both silvicultural systems. Its efficiency increases with light intensity, so its adaptation ability to light increase is better than in fir. The lower efficiency of fir in exploiting high-intensity solar radiation compared to beech may be a competitive disadvantage in large canopy gaps, which could limit species recruitment to the forest understory or small gaps, especially in admixture with beech. It is not certain if silver fir would be able to efficiently prosper in a beech-predominating environment and faster changes of light conditions, since beech expresses more plasticity, which silver fir is not able to follow to such an extent. The leaf efficiency depends on photosynthetic induction and is inverse to the duration of the lightfleck (Küppers et al., 1996). Seedlings that grow in conditions of low irradiance are better adapted to utilize dispersed light of low intensity (Hal and Aarsen, 1997) but require longer induction period when illuminated by a fleck of direct light (Pearcy et al., 1994). Ecological differences among positions within gaps may also be partly due to the variability of factors that do not depend on irradiation, such as micro-relief, soil substrates and woody debris.

In order to favour fir, gaps with low direct light levels should be created, increasing the proportion of A and C microsites with predominating diffuse light conditions; existing gaps should be extended towards the southern gap edge (Čater et al., 2014). Young fir trees would benefit more in A and C types of microsite categories, with a predominant diffuse light component and the preservation of smaller gaps and fragmented canopy structure, found also in the old growth reserves, as confirmed in four highest elevation belts (Table 4).

4.2 Comparison between silvicultural systems

Many studies have emphasized the management system as a key factor for the distribution of tree species and also for tree decline (Heuze et al., 2005b; Manetti and Cuttini, 2006). Dinaric beech and fir forests

were gradually transformed from old-growth conditions and have never experienced clear cutting. They were managed with continuous-cover silvicultural systems, especially with single-tree selection systems, irregular shelterwood or their combination (Mlinšek, 1972, Bončina, 2011).

In Dinaric silver fir and beech forests the proportion of fir artificially increased from the end of 19th century for economic reasons. A significant expansion of beech in once pure fir stands has been evidenced because of different forest management practices or main species alteration (Mlinšek, 1964). In the Slovenian Dinaric mountains after WWII the selection system was gradually extended. It became known as the “freestyle silviculture” (Mlinšek, 1996; 1968), as some elements of small-scale irregular shelterwood system were included into it to provide better adaptation of different tree species to the climate conditions and to reduce the fir decline (Diaci et al., 2011). It combines different felling and tending approaches to allow adaptation to small-scale variability of site, stand and management conditions (Schütz et al, 2016).

Differences between two silvicultural systems in our study proved significant in different shares of microsite light categories over lower elevation belts, while in the four highest elevation belts the proportion of microsite categories in analysed gaps showed almost identical shares in both areas (S and I, respectively) indicating similar composition of the forest edge, regardless of the silvicultural system. Both shares in managed forests were also similar to proportion of microsities in old growth reserve, located in the highest elevation belt (Tables 6, 7), mimicking natural processes and were also in accordance with the concept of small-scale irregular shelterwood system.

Maintaining the single-tree selection system within the region would help to preserve the competitive ability of fir, while the irregular shelterwood system proved as more light-efficient for both species (Čater and Levanič, 2013). As beech and fir's advance regeneration often outcompetes less shade tolerant species, selection system practiced over longer periods leads to a decline in species diversity especially for the shade intolerant tree species (Keyser and Loftis 2012). Different silvicultural systems with irregular stands and patchy mosaic would therefore be more appropriate (Raymond et al., 2009). However, the retrospective study of Adamič et al. (2016) confirmed that the long-term application of spatially and temporary diversified uneven-aged management (i.e. freestyle silviculture) on Slovenian sites did not result in reduced tree species diversity. It suggested preservation of shade-tolerant as well as mid-tolerant tree species, which may further imply the importance of both gap dynamics and tending measures for preservation of species richness (Adamič et al. 2016).

In our opinion, the similarity of microsite shares in highest elevation belt proves efficient silvicultural approaches in both systems, that primarily respect natural constraints to achieve long-term ecologically and economically well-tuned silvicultural goals. In such way, both approaches reflect identical structure that optimizes co-existence of beech and silver fir that is nearest to the natural approach.

5. Conclusions

Results of this study confirm fir's competitive advantage over other species within a single tree selection system and more light-efficient physiological and morphological responses of beech and fir in the irregular shelterwood system. Our conclusions emphasize the importance of smaller gaps, in contributing to an increased competitive advantage of fir in mountainous, mixed-species Dinaric forests.

- We confirmed fir's advantage in diffuse light conditions on a wider spatial scale and altitudes;
- most of the fragmented area within single tree selection system was located between 300-699 m and between 100-499 m in the irregular shelterwood system;
- smallest share of forest edge area in both systems was found in the highest elevation belt;
- width of the forest edge belt did not affect the proportion of the microsite categories;
- with increasing altitude shares of forest edge (i.e. microsities) became equal in both areas and similar to the proportion in old growth reserve.

Not only favoring of microsities where fir can prosper better compared to other key species, but also application of silvicultural approaches that proved efficient in promotion of fir may contribute to stabilize and preserve current structure in high Dinaric karst forests, especially in fir-beech forest types, where the progress of beech and fir's regression are becoming evident.

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