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RELATION BETWEEN PHOTOSYNTHETIC PHOTON FLUX DENSITY (PPFD) AND GROWTH OF SILVER FIR (*ABIES ALBA* MILL.) SEEDLINGS IN A FOREST STAND DOMINATED BY SPRUCE [*PICEA ABIES* (L.)H.KARST.] IN THE SUDETY MTS (SW POLAND)

ABSTRACT: The relations between Photosynthetic photon flux density (PPFD) and both the number of silver fir (*Abies alba*) seedlings per unit area and their height growth were investigated. The study was carried out in the Sudety Mts (SW Poland, 50°28'N, 16°19'E), in a forest stand dominated by spruce (*Picea abies*), growing on site of mixed broad-leaved mountain forest. This site type is very commonly colonized by silver fir in this part of Europe. The number of fir seedlings per unit area decreased with growing PPFD values, whereas seedling height increased. Our results suggest that greater access of sunlight, at least within the recorded PPFD range (0–40% of full irradiation) improves the growth conditions of fir seedlings but at the same time the spread of grasses (mainly *Deschampsia flexuosa*) inhibits the rooting and development of new seedlings. Thus regenerative felling should be conducted in forest stands in these places where fir seedlings are numerous.

KEY WORDS: silver fir, natural renewal, growth, light

1. INTRODUCTION

Silver fir (*Abies alba* Mill.) belongs to the species that normally renew under the forest canopy. The variety of conditions in the forest interior makes all the issues connected with the renewal process of this tree quite complex. One of the most important factors affecting the renewal of the fir population is light. According to Leibundgut (1976) the light supplies are more important to young trees than soil conditions. Fir is commonly classified as a shade-tolerant tree [in European conditions it ranks second in this respect, after yew (*Taxus baccata* L.)] and the range of light conditions in which it may occur is wide (Ellenberg 1979, Zarzycki *et al.* 2002). This does not mean, however, that light exerts little influence on its life processes. On the contrary, as it is shown in publications concerning this issue, light plays an important role especially in the process of renewal of fir populations (Chmelař 1959, Korpel and Vinš 1965, Boni *et al.* 1978, Giannini and Tascione 1978, Magnuski *et al.* 2001). On the other hand, light conditions are one of the environmental factors that we can change to a large extent, influencing in this way the process of renewal. Although problems connected with fir reproduction are discussed in numerous publications, the direct relationships between growth rate and number of fir seedlings on the one hand and light conditions on the other have not been established and the optimal conditions for their growth have not been explicitly determined. The majority of studies indicate that the influence of light is considerable but it depends on many other factors, such as climate (Jaworski and Zarzycki 1983), soil conditions (Jaworski and Zarzycki 1983, Filipiak *et al.* 2003), exposure (Korpel and Vinš 1965), as well as the composition and structure of the forest stand (Boni *et al.* 1978, Jaworski 1979, Malavasi and Perry 1993, Dobrowolska 1998). Origin of seed material may also play a part (e.g. Leibundgut 1978, Gunia 1999). All these are accompanied by different requirements of young fir trees depending on their age. According to Chmelař (1959), individuals aged 0–1, 1–4 and 4–8 years differ considerably in ecological requirements. The undergrowth (i.e. specimens higher than 0.5 m) has different light requirements than a thicket. This shows that the results of research on the influence of light on growth must be referred to specific conditions and the developmental stage of young trees.

Silver fir is a Central European, mountain species. In the southern parts of its distribution it grows exclusively in the mountains at elevations of about 800–900 m and the most elevated stands occur at 2000–2100 m in the Pyrenees, Apennines and in the mountains of Bulgaria. In the northern parts of the range the species grows also in the lowlands.

As recently as 200 years ago, fir was a common tree in the Sudety Mts, at present, however, it is rare and very dispersed in that area. First of all this is due to forest economy unfavourable to the fir, prevailing from the late XIX century to the middle of the XX, which promoted spruce monocultures and short period of forest renewal. Another important factor was the high level of industrial air pollution in this region particularly, especially a high content of SO_2 derived from burning brown coal in power stations in 1960–1990. The latter factor had a negative influence not only on the number of fir trees, but also on their health. At present, however, the SO_2 level in the air is many times lower than 10 years ago, and very distinctive revitalising of older fir trees is observed (Zientarski *et al.* 1994, Vancura *et al.* 2000, Filipiak and Ufnalski 2004). This process is accompanied by an increase in cones production as well as a better natural renewal of fir populations. In the latter case, the most important problem is the low participation of fir in the Sudety Mts forest stands, and, consequently, the low number of seedlings from natural sowing. This fact is the reason for the great interest in the factors affecting the intensity and efficiency of self-sowing, especially the factors that can be easily manipulated, such as light (Filipiak 2002, Filipiak and Barzdajn 2004).

The aim of this study was to determine the relationships between the amount of photosynthetically active light reaching the particular places at the forest floor and both the growth rate and number of fir seedlings. The selected forest stands represented the conditions typical for most fir stands in the Sudety Mts and common in other, particularly northern, parts of the natural range of this species (Northern Alps, Black Forest, Ore Mountains, Carpathians).

2. STUDY AREA

The study was carried out in the central part of the Sudety Mts (SW Poland) in National Park of Stołowe Mountains (50°28'N, 16°19'E) in a forest stand (total area 21 ha) situated at the altitude of 690–720 m a.s.l.

The terrain is moderately inclined, with western or south-western exposure. The soil is acid brown developed from silty loam on a weathered sandstone, the humus is of moder type. The forest stand is moderately dense and consists of spruce (*Picea abies*) (70–80%), fir (*Abies alba*) (20–30%), and infrequent beech (*Fagus sylvatica*) trees. The specimens forming the upper tree layer were 80–120 years old. The forest site type was classified as mixed broad-leaved mountain forest ("LMG"), which is commonly colonized by fir, as about 70% of individuals of this species in the Sudety Mts grow on such sites (Filipiak and Kosiński 2002).

3. MATERIAL AND METHODS

The objects of the study were self-sown fir seedlings. In order to examine the process of fir stand renewal, 6 square plots were established, with the sides 10 m long. The above mentioned plots are characterized by nearly the same habitat conditions (soil, exposure, forest stand type, etc.), typical for the given region and altitude zone (see above). Each of those plots was divided into 100 squares with the sides 1m long. Therefore the total number of squares was 600. On each square (1m × 1m) the number of seedlings was determined and their height was measured.

Photosynthetically active light (photosynthetic photon flux density PPFD) was measured with a one-metre-long Line Quantum Sensor (Apogee Inc.) with 20 sensors built in every 5 cm. The meter showed the average value of light intensity (recorded by the 20 sensors). The measurements were taken 15–20 cm above the ground (average height of seedlings). In each square (1m × 1m), two measurements were taken perpendicularly to the sides of the square and the average was calculated (Ter-Mikaelian *et al.* 1997). The measurements of light were taken on 4th and 5th September 2002, both in cloudy and in sunny weather, for both dispersed and direct light (Messier and Puttonen 1995; Parent and Messier 1996; Machado and Reich 1999). At the same time, a Watch Dog recorder (Specmeters Inc.) placed in the open area took measurements of light at one-minute intervals. By comparing values of light intensity in the open area and in the examined plots at the same time, the per cent values of relative light intensity reaching particular squares were calculated. On the basis of data thus obtained, all the squares, including those without seedlings, were classified into 8 light classes: 0–5%, 6–10%, 11–15%, 16–20%, 21–25%, 26–30%, 31–35%, 36–40%. The number of seedlings in each of the 8 classes of PPFD distinguished as above was summarized and the average number of seedlings per m^2 was calculated. Dependence of: 1) number of seedlings per square metre and 2) average height increment of seedling per square metre with relative PPFD were tested by regression analysis (Underwood 1997, Zar 1999) with the use of JMP software (JMP, SAS Institute).

On each square (1m × 1m) the degree of cover of the forest floor by the herb layer was estimated visually. Three classes of cover were distinguished: class I, 1–35%; class II, 36–70%; and class III, 71–100%. The significance of differences in mean number of fir seedlings per unit area between these three classes was assessed by the χ^2 test.

4. RESULTS

As a result of the study, 672 seedlings were found on all the plots (from 31 to 191 per plot). The age of seedlings ranged from 1 to 9 years, and the height ranged from 2 to 28 cm (on average 6.8 cm).

When assessing the relationships between seedling height and PPFD, and between height increment and PPFD, we used only data from 398 squares (1m × 1m) where seedlings were found. When assessing the relationships between seedling number per m^2 and PPFD, and between seedling number per m^2 and degree of cover of the soil by grasses, we took into account all 600 squares. The number of squares in the light classes ranged from 21 squares (class: 35–40% of full irradiation) to 136 squares (class 5–10% of full irradiation). The number of squares in the grass cover classes varied from 155 squares to 248 squares.

A comparison of the collected data showed that with increasing light intensity, the height of seedlings and the length of the last annual increment of apical shoots increased significantly (Fig. 1 and 2).

An opposite relationship was observed in respect of the number of seedlings per unit area, which decreases considerably with increasing light intensity (Fig. 3).

Data presented in Fig. 4 suggest that the number of fir seedlings per unit area decreases with increasing degree of cover of the forest floor by grasses: *Deschampsia flexuosa* and *Calamagrostis* spp. The differences between distribution patterns of number of fir seedlings per unit area in three distinguished classes of cover, are significant (χ^2 test, $P \leq 0.05$).

5. DISCUSSION

In the conditions of the studies and the range of PPFD taken into consideration (0–40%), we observed a positive influence

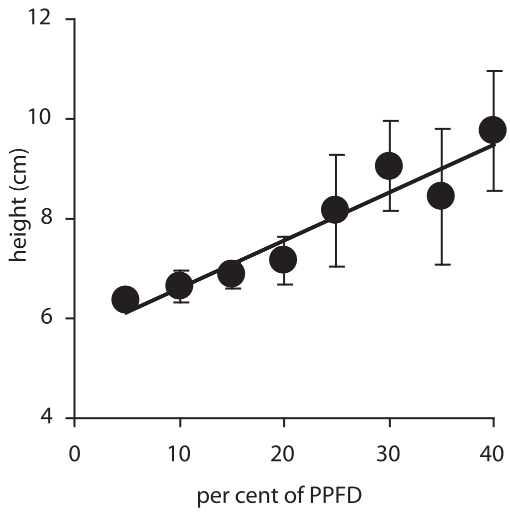

Fig. 1. Photosynthetic photon flux density (PPFD) at the forest floor (expressed as % of open air incident light intensity) *vs*. mean height of fir seedlings on the studied plots in the Sudety Mts (R^2=0.91, *P*=0.0003, y=0.48x + 5.65).

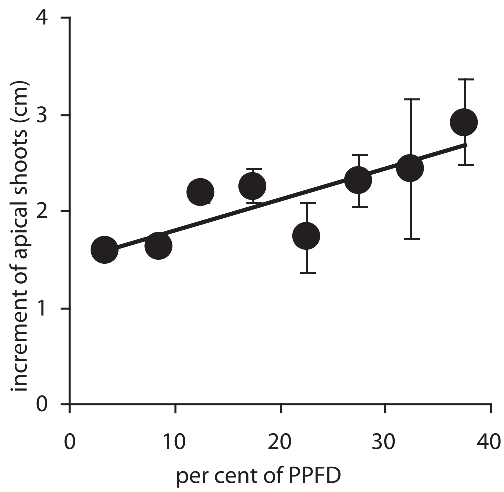

Fig. 2. Photosynthetic photon flux density (PPFD) at the forest floor (expressed as % of open air incident light intensity) *vs*. annual increment of the main shoot of fir seedlings on the studied plots in the Sudety Mts (R^2=0.70, *P*=0.009, y=0.03x + 1.47).

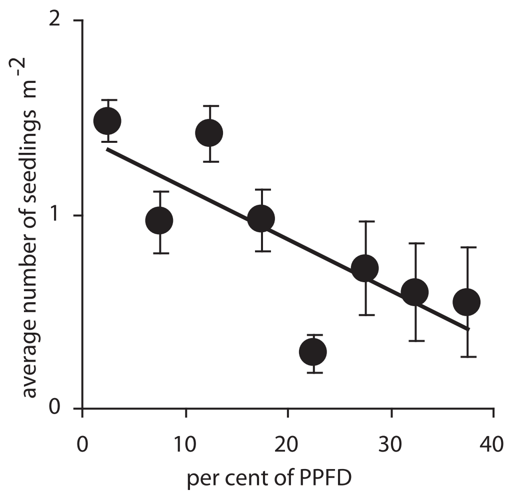

Fig. 3. Photosynthetic photon flux density (PPFD) at the forest floor *vs*. number of fir seedlings per unit area on the studied plots in the Sudety Mts (R^2=0.60, *P*=0.03, y=–0.13x + 1.47).

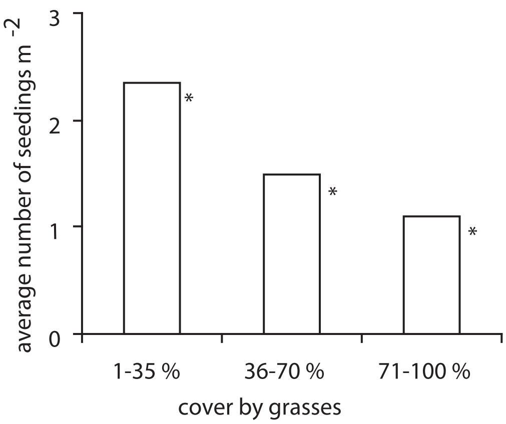

Fig. 4. Number of fir seedlings per unit area *vs*. degree of cover by grasses, *Deschampsia flexuosa* and *Calamagrostis* spp. on the studied plots in the Sudety Mts. The significant differences *P* ≤0.05 marked with asterisk.

of the light accessibility on seedling height and size of the last annual increment. This is consistent with the results of the majority of publications on this subject. Earlier research indicate that the biomass of seedlings increases with the increase of PPFD irrespective of species and shade tolerance of seedlings (Hiroki and Ichino 1998, Reich *et al*. 1998, Valio 2001). This applies also to silver fir. With the increasing access of light, seedling height and weight increase, although they vary with seedling age, site fertility, water content in the soil, species composition of the canopy, or other factors (Korpel and Vinš 1965, Giannini and Tascione 1978, Jaworski and Zarzycki

1983, Dobrowolska 1998, Robakowski and Wyka 2003).

Interesting are results concerning the relation between light and number of seedlings per area unit. As light intensity increased, the density of seedlings (especially the youngest ones) notably decreased. This seems to be connected with the fact that the greater accessibility of light results in increased competition among the herbaceous plants as well as among seedlings of other tree species, which are more light-demanding. Such competition may significantly hinder the development of young free-standing fir seedlings, despite the fact that a greater accessibility of light results in an apparent improvement of the growth conditions of individual fir seedlings (Veblen 1989, Lautenschlager 1999).

On the studied plots, the main component of the ground layer is wavy hair grass *Deschampsia flexuosa* – a low, but very dense grass, which dead and live leaf blades lie mostly on the ground, forming thick, cushion-like patches in brighter parts of the forest floor. These patches do not constitute a great competition for saplings 12–15 cm tall. However, they seem to be able to hinder effectively the development of the youngest seedlings by intensely shading them and mechanically obstructing their growth by the dense, tangled network of dead and live blades. This network may also effectively impede the access of the large fir seeds to the soil surface, making it impossible for them to germinate and exposing them to the dangers of drying and being eaten by birds or rodents. Earlier research (Jaworski 1973, Jaworski and Zarzycki 1983) show that light conditions in the dense undergrowth are on the level rarely exceeding the light minimum for fir, determined for the youngest seedlings at the level of 4–5% (Bezačinski 1960, Korpel 1975, Jaworski and Zarzycki 1983). It is noteworthy that in the mountains of Central Europe *Deschampsia flexuosa* is common in moderately dense forest stands dominated by spruce.

In places exposed to direct sunlight, the soil is drier, which may also exert a negative influence on seed germination and early seedling growth (Becker *et al*. 1988, Battaglia *et al*. 1999).

Larger numbers of seedlings growing under the woodland canopy than in open area were found also in other, mainly shade-tolerant species of the temperate and warmer climatic zones (Veblen 1989, Lautenschlager 1999, Slocum 2001). According to some authors (Levine 1999, Pages and Michalet 2003), this is due to the "indirect facilitation effect". The canopy trees, which limit the access of sunlight to the forest floor, indirectly facilitate seedling growth by eliminating light-demanding competitors and maintaining a high humidity of the upper layers of the soil. This advantages are greater than the disadvantages of the limited amount of sunlight. The studies cited above were conducted in a system: woodland – small clearing (covering several acres). Our results suggest that this effect occurs also under gently open canopy formed by trees, when light conditions are not so different.

Similar results were reported by Iszkuło and Boratyński (2005) for yew seedlings. However, the advantages of strong shading seem to dominate over its disadvantages only in the case of the youngest yew seedlings (1–2 years old), as only this age group was abundant under such conditions. Older seedlings preferred places with larger light access (Iszkuło and Boratyński 2005). This may indicate that many seedlings die when shaded strongly because their light demands increase with age, which is a widespread phenomenon (e.g. Jaworski and Zarzycki 1983, Zhu *et al*. 2003). In a study conducted by Pages and Michalet (2003) in the lower mountain zone of the French Alps, several-year-old seedlings of spruce, beech, oak, maple and fir grew much better in a clearing, despite a strong competition with *Molinia coerulea* (PPFD 15% of full sunlight), than under the woodland canopy (PPFD 3–5% of full sunlight). Thus it seems that the above conclusion about yew seedling applies also to fir seedlings. It seems that we have here the example of "seeds – seedlings conflict" (Shupp 1995), although in a form: "very young seedlings *versus* older seedlings".

6. CONCLUSION

The results presented here imply that in order to promote self-sowing of fir it is best to maintain a litter cover on the soil in the forest stand and light access to the forest floor within 6–15% of full light (in these conditions the development of *Deschampsia flexuosa* is unlikely). In places where a sufficient number of seedlings occurs, it is recommended to increase the access of light. It should be initially up to 15%, and then to 30% and even 50% (Bezačinski 1960, Korpel 1975, Giannini and Tascione 1978, Jaworski and Zarzycki 1983). An increased accessibility of light to fir seedlings results in greater growth increments and competitive ability; it also satisfies the demands increasing with age.

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