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# EFFECTS OF IRRADIANCE ON BIOMASS ALLOCATION AND NEEDLE PHOTOSYNTHETIC CAPACITY IN SILVER FIR (*Abies alba* MILL.) SEEDLINGS ORIGINATING FROM DIFFERENT LOCALITIES

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## Introduction

Decline events have been repeatedly reported in Europe for silver fir (*Abies alba* MILL.) since the seventeenth century [DOBROWOLSKA 1998]. However, the main cause of this susceptibility of silver fir to decline remains still unclear [BERNADZKI 1983]. This species is known to be highly sensitive to drought, to low or excessively high temperatures, to air pollution and to excessive irradiance. It is considered to be one of the most shade-tolerant European tree species [JAWORSKI 1995]. An improved knowledge of the main ecophysiological features of silver fir is of importance in attempting to elucidate the reasons of its susceptibility to decline.

In this study we documented the acclimation potential of silver fir seedlings to a wide range of solar irradiance, and estimated the responses of biomass allocation, leaf structure, total nitrogen and chlorophyll content in leaves, and photosynthetic capacity (estimated as the maximal carboxylation rate, $V_{cmax}$ and the maximal light driven electron flow $J_{max}$ according to the model by Farquhar). Based on these photosynthetic parameters, the potential irradiance related modulation of nitrogen allocation to different photosynthetic processes (carboxylation – $P_C$, bioenergetics - $P_B$, light harvesting - $P_L$) was quantified.

We expected the photosynthetic parameters of this extremely shade-tolerant species to be different in comparison with those of light-demanding trees. In addition, we tested whether seedlings originating from different localities in the Polish mountains displayed different abilities to acclimate growth and photosynthetic response to irradiance levels.

## Material and methods

Three provenances from the Sudety mountains (seeds collected at 520, 620 and 750 m elevation a.s.l.) and 3 from the nursery in Carpathian Mountains (seeds collected at 145 m in the strict reserve „Jata", 345 m in Roztoczański National Park and at 945 m a.s.l. in the strict reserve „Łabowiec" near Nawojowa) were used. Four-year-old seedlings originating from these localities were transplanted during Spring 1999 to 10 dm³ pots (sand/peat, 2/1 v/v, fertilization: 5 g·dm$^{-3}$ slow release Nutricot N/P/K 13/13/13 every Spring) and grown at Champenoux, Nancy (France) under one of 4 different light regimes: 100% – full irradiance; 48, 18 and 8% of incident irradiance, imposed with neutral shade nets. Measurements were made at the end of Summer 2000. The acclimation had lasted 2 full growing seasons.

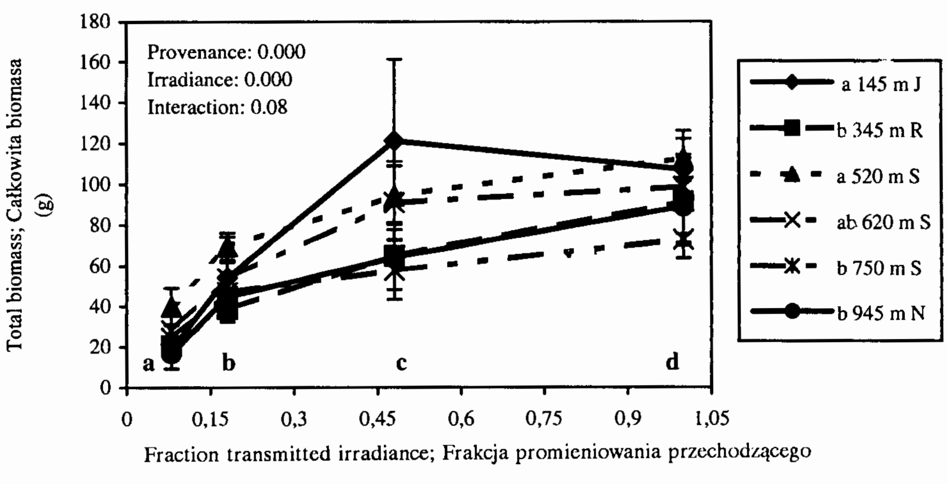
Response curves of net $CO_2$ assimilation rate *vs.* intercellular $CO_2$ were generated under saturating irradiance (1500 $\mu$mol·m$^{-2}$·s$^{-1}$) on twigs *in situ*, using a portable gas exchange system (LiCor 6400). These curves were used to adjust $V_{cmax}$ and $J_{max}$ as described by DREYER et al. [2001]. Five seedlings per provenance and per treatment were used. The fraction of total nitrogen allocated to each photosynthetic process was calculated as described by NIINEMETS and TENHUNEN [1997]. Chlorophyll content in needles was estimated spectrophotometrically using extracts of needles in DMSO [BARNES et al. 1992]. Dried needles were ground to a fine powder for total leaf nitrogen content analyses using gas chromatography.

Plant parts were separated into needles, stem and roots, and then washed, dried and weighed for biomass computation.

The data were analysed using two-way ANOVA with interaction at $p < 0.05$ (p – significance level) followed by Tukey's *a posteriori* test with global $p < 0.05$. Pearson's coefficients (r) with the values of probability (P) at $p < 0.05$ were also calculated to show linear relationships. The software Statistica 5.5 was used for all the analyses.

## Results and discussion

Both total biomass and biomass allocation to different compartments were modified by irradiance levels: the whole seedling biomass (Figure 1) and the root/seedling biomass ratios responded positively to increasing irradiance ($r = 0.767$, $P = 0.000$ and $r = 0.838$, $P = 0.00$, respectively) while the shoot/root bio-

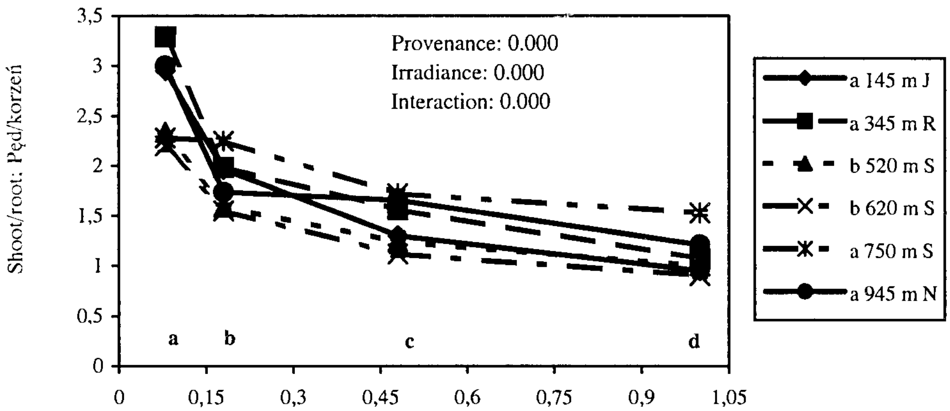


„Provenance"; Proweniencja, „Irradiance"; Promieniowanie, „Interaction"; Interakcja

J – seedlings originating from the strict reserve „Jata", 145 m a.s.l. (northern extremity of *Abies alba* continuous range); sadzonki pochodzące z rezerwatu ścisłego „Jata", 145 m n.p.m. (północny kraniec ciągłego zasięgu *Abies alba*)
R – Roztoczański National Park, 345 m a.s.l.; Roztoczański Park Narodowy, 345 m n.p.m.
S – Sudety Mountains, 520, 620, 750 m a.s.l.; Sudety, 520, 620, 750 m n.p.m.
N – Carpathian Mountains, the strict reserve „Łabowiec" near Nawojowa, 945 m a.s.l.; Karpaty, rezerwat ścisły „Łabowiec" niedaleko Nawojowej, 945 m n.p.m.

Fig. 1. Total dry biomass (means ± standard deviations) of silver fir seedlings from six provenances grown at different levels of solar irradiance. The effects of provenance and irradiance were analysed using two-way ANOVA. Shared letters indicate lack of statistical differences between provenances (lowercase letters in the legend) or between irradiance levels (letters above x-axis) as indicated by Tukey's *a posteriori* test at $p < 0.05$ (p – significance level)

Rys. 1. Całkowita sucha biomasa sadzonek jodły pospolitej (średnie ± odchylenie standardowe) sześciu proweniencji rosnących w warunkach różnych poziomów promieniowania słonecznego. Wpływ proweniencji i napromieniowania określono przy pomocy dwuczynnikowej analizy wariancji. Te same małe litery w legendzie oznaczają brak statystycznych różnic między proweniencjami lub między poziomami promieniowania (litery nad osią x) na podstawie testu *a posteriori* Tukey'a na poziomie istotności $p < 0.05$



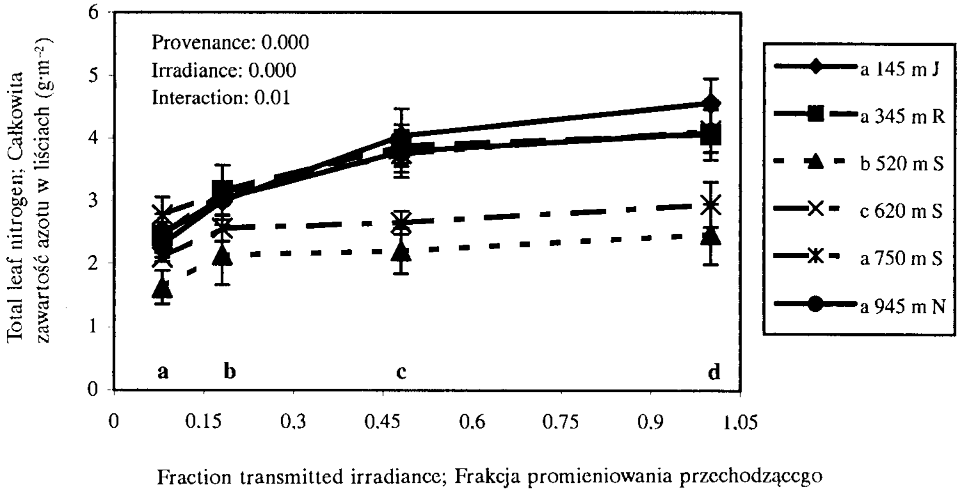

Explanations see Fig. 1; Objaśnienia jak na rys. 1

Fig. 2. Shoot/root biomass ratio in silver fir seedlings from six provenances growing under different irradiance. For further explanations see Figure 1

Rys. 2. Stosunek części nadziemnej do korzenia sadzonek jodły pospolitej sześciu proweniencji rosnących w różnych warunkach promieniowania. Inne objaśnienia patrz rys. 1

mass ratio decreased ($r = -0.838$, $P = 0.00$), (Figure 2). The leaf mass to area ratio increased with irradiance (data not shown). Total nitrogen concentration was independent of irradiance when calculated on dry mass basis but increased on a leaf area basis ($r = 0.59$, $P = 0.000$), (Figure 3). The reverse was noticed for total chlorophyll concentration (chlorophyll a + b), (data not shown). Such responses and their magnitude were similar to what had been observed with broadleaved seedlings [DREYER et al. 2001].

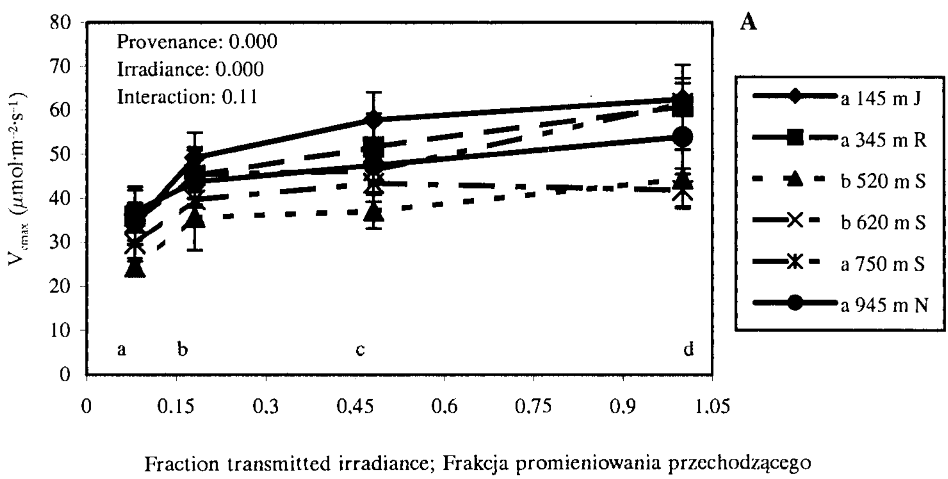
Both $V_{cmax}$ and $J_{max}$ increased with irradiance (Figure 4a, b) but the $J_{max}/V_{cmax}$ ratio was stable. The relative nitrogen allocation values to the different components of photosynthetic apparatus were: carboxylation 12 ± 2% (mean ± SD) of total N (range 8 to 17%), bioenergetics 3 ± 0.4% (2–4%) and light harvesting 7 ± 3% (4–20%). These values are rather lower when compared to the $P_C$, $P_B$, $P_L$ obtained for deciduous trees [DREYER et al. 2001]. The relative allocation of nitrogen to carboxylation and bioenergetics were not modified by increasing irradiance, but allocation to light harvesting decreased.

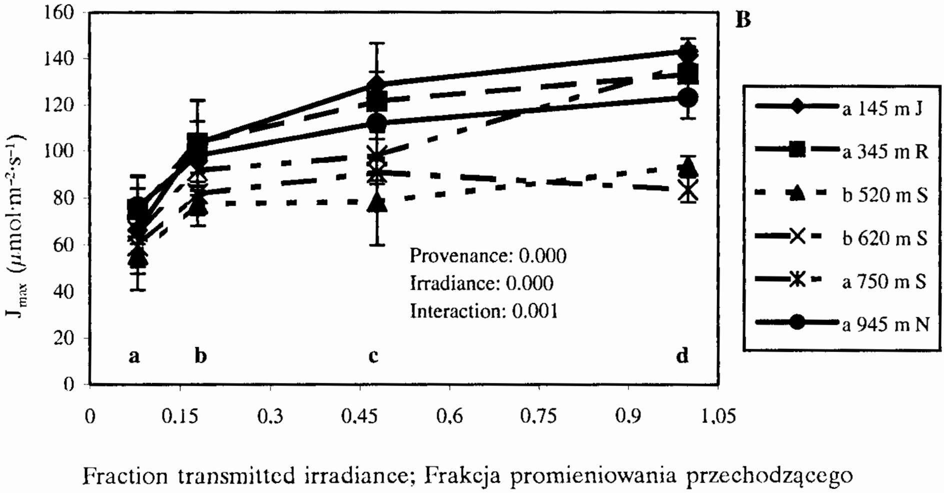



Explanations see Fig. 1; Objaśnienia jak na rys. 1

Fig. 3. Total leaf nitrogen per leaf area in needles of *Abies alba* seedlings. For further explanations see Figure 1

Rys. 3. Całkowita zawartość azotu w igłach sadzonek *Abies alba*. Pozostałe objaśnienia patrz rys. 1






Explanations see Fig. 1; Objaśnienia jak na rys. 1

Fig. 4a, b. Maximal carboxylation rate ($V_{cmax}$) – (4a) and maximal light driven electron flow ($J_{max}$) – (4b) in needles of silver fir seedlings. For further explanations see Fig. 1

Rys. 4a, b. Maksymalna prędkość karboksylacji ($V_{cmax}$) – (4a) i maksymalny przepływ elektronów ($J_{max}$) – (4b) w igłach sadzonek jodły. Pozostałe objaśnienia patrz rys. 1

## Conclusions

The photosynthetic apparatus of *Abies alba* appeared to undergo acclimation to increasing irradiance by reducing the investment of nitrogen in light harvesting antennae.

The effect of seedling provenance on biomass allocation, leaf structure and all photosynthetic parameters was statistically significant. No clear trend based on elevation or on the area of the provenances could be detected. In addition, the plasticity in the responses to irradiance was rather similar for each provenance, however some differences were found basing on statistically significant interactions between provenance and irradiance.

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**Key words:** *Abies alba*, photosynthesis model, maximal carboxylation rate, maximal light driven electron flow, nitrogen allocation, biomass allocation

## Summary

In this study, we determined the effects of an acclimation of silver fir (*Abies alba* MILL.) seedlings from six provenances to different levels of solar irradiance on: biomass allocation in seedlings, leaf structure, total nitrogen and chlorophyll content in the leaf, maximal carboxylation rate and maximal light driven electron flow. Based on these photosynthetic parameters, the amount of nitrogen allocated to each process (carboxylation, bioenergetics and light harvesting) was estimated. The photosynthetic apparatus of *Abies alba* appeared to undergo acclimation to increasing irradiance by reducing the investment of nitrogen in light harvesting antennae. The effect of seedling provenance on biomass allocation, leaf structure and all photosynthetic parameters was statistically significant. No clear trend based on elevation or on the area of the provenances could be detected. In addition, the plasticity in the responses to irradiance was rather similar for each provenance, however some differences were found basing on statistically significant interactions between provenance and irradiance.

# WPŁYW PROMIENIOWANIA NA ALOKACJĘ BIOMASY I WYDAJNOŚĆ FOTOSYNTETYCZNĄ IGIEŁ SADZONEK JODŁY POSPOLITEJ (*Abies alba* MILL.) POCHODZĄCYCH Z RÓŻNYCH POŁOŻEŃ GEOGRAFICZNYCH

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Słowa kluczowe: *Abies alba*, model fotosyntezy, maksymalna prędkość karboksylacji, maksymalny przepływ elektronów, alokacja azotu, alokacja biomasy

Streszczenie

Na podstawie analizy alokacji biomasy sadzonek, specyficznej masy igieł, całkowitej zawartości azotu i chlorofilu w igłach oraz pomiarów maksymalnej prędkości karboksylacji oraz maksymalnego przepływu elektronów określono efekt aklimatyzacji sadzonek jodły pospolitej (*Abies alba* MILL.) sześciu prowe-niencji do różnych poziomów promieniowania słonecznego. Obliczono także wielość frakcji azotu przemieszczanego do poszczególnych procesów składających się na fotosyntezę (karboksylacja, procesy bioenergetyczne, pochłanianie energii świetlnej). Aparat fotosyntetyczny jodły aklimatyzuje się do rosnącego poziomu promieniowania słonecznego zmniejszając „inwestowanie” azotu w budowanie białek absorbujących światło. Wpływ proweniencji na alokację biomasy, strukturę igieł i parametry fotosyntezy był statystycznie istotny. Plastyczność reakcji w odpowiedzi na promieniowanie była podobna dla wszystkich proweniencji, jednak pewne różnice stwierdzono na podstawie statystycznie istotnych interakcji między proweniencją a promieniowaniem.

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