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ORIGINAL ARTICLE

Responses to temperature and shade in *Abies alba* seedlings from diverse provenances

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Abstract

Intraspecific variability in responses to temperature and shade was studied at Champenoux, north-eastern France, with seedlings from five Polish provenances of silver fir (*Abies alba* Mill.). Acclimation of photosynthesis to temperature was investigated in seedlings exposed to 10, 25 and 35°C in a climate chamber for 1 week. During two growth seasons, a population of seedlings was grown in the nursery under four different irradiance regimens: 100, 48, 18 and 8% of natural irradiance. Maximum carboxylation rate (V_{cmax}), maximum light driven electron flow (J_{max}) and maximum net carbon dioxide assimilation rate (A_{max}) measured at 25°C increased with population altitude. One week of exposure to 35°C caused discoloration and massive needle shedding. After 2 years' acclimation to different levels of irradiance, a significant interprovenance variability was evidenced in growth, total biomass, biomass allocation and photosynthetic performance. This study provided evidence for the existence of functional variation among the examined provenances.

Keywords: Biomass allocation, functional traits, nitrogen allocation, photosynthetic capacity, silver fir.

Introduction

Silver fir (*Abies alba* Mill.) occurs in central, southern and western Europe, mostly in the mountains. From a central nucleus in the Alps, Vosges, Jura, Black Forest (southern Germany) and Bohemia (Czech Republic), the natural distribution area branches out into three main directions: (1) a discontinuous line down the Apennines; (2) a continuous line from the Dinaric Alps to the Pindus and the Rodopi Mountains (Greece); and (iii) a last line to the central European mountains. Completely spatially disconnected populations exist in Poland, north-western and central France, Corsica and the Pyrénées (CABI, 2005). In Poland, silver fir grows naturally in southern mountains and uplands, from 500 to 1100 m a.s.l. (Gostynska-Jakuszevska, 1972; Boratynski, 1983; Filipiak & Barzdajn, 2004). An isolated population grows in Białowieza Forest (the natural reserve “Cisówka”), which is around 150–170 km from Siedlce Uplands, the northern limit of the continuous range (Gostynska-Jakuszevska,

1972). However, the indigenous or anthropogenic origin of this population has not been proved (Srodon, 1983). In Siedlce Uplands, the population in the natural reserve “Jata” is regarded as the northernmost natural fir population, situated closer to the northern limit of the continuous range than that in Białowieza Forest (Gostynska-Jakuszevska, 1972; Jaworski, 1995). As a lower mountain species, *A. alba* occurs in the Swietokrzyskie Mountains as well as in lower situated sites in the Sudety and the Carpathian Mountains. In Poland, the most favourable growth conditions are found in the Carpathians (“Beskid Sadecki” and “Niski”) and in the Carpathian foothills. The species covers a relatively small geographic range in comparison with more economically important conifers such as Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* Karst.). This may reflect strict ecological requirements and could imply a relatively low functional diversity.

Abies alba is one of the most shade-tolerant European tree species; it is able to survive under

deep shade during several years and to respond rapidly to a clearing in the canopy above (Brzeziecki & Kienast, 1994). Normal growth during the first 2 years requires around 5% of incident irradiance. Five-year-old saplings may be found down to 8% of full irradiance in natural stands. Later on, at 5–15 years, young trees tolerate shade ranging from 10 to 33% with an optimum between 15 and 25% (Jaworski, 1995). Silver fir performs best in a climate characterized by high air humidity and low temperature amplitudes. A mean annual rainfall of 600 mm marks the lower limit of its natural range. The best growth occurs where mean annual rainfall exceeds 1500 mm and mean annual temperature is about 9°C (CABI, 2005). *Abies alba* does not tolerate minimum temperatures falling below –20 to –25°C. Decreases of temperature to –27°C caused serious frost damages in fir stands (Jaworski & Zarzycki, 1983). Low temperatures in winter, spring frosts and water deficit are the main factors that determine the northern and eastern limits of its natural range.

Intraspecific diversity of ecophysiological traits in silver fir has not yet been clearly identified (Leibundgut, 1978). However, a large diversity in phenology was detected among populations from the whole range (Arbez, 1969). The degree of intraspecific diversity seems to decrease from south to north; the Mediterranean populations display a large diversity and Quezel (1998) even suggested distinguishing European from Mediterranean populations. This gradient was apparently also reflected in a gradient of decline during the 1980s: the less diverse populations of continental Europe were much more affected by atmospheric pollution than those from the southern Alps, the Carpathians and the Mediterranean basin (Larsen, 1986). During the past decade, improved health and frequent natural regeneration were recorded in fir stands in France and Poland (Becker et al., 1994; Dobrowolska, 1998; Zawada, 2001).

In Poland, silver fir grows naturally in southern mountains and uplands, from 500 to 1100 m a.s.l. (Gostynska-Jakuszevska, 1972). Provenance tests revealed a large variability among provenances from the Carpathians and the Sudety Mountains, the former displaying larger growth (Gunia, 1986; Korpel & Paule, 1984). Populations of silver fir showed large genetic variation and diversity with values comparable to those described in Scots pine populations (Mejnartowicz, 1983). Populations from the Sudety Mountains were characterized by much lower genetic diversity than Carpathian populations (Mejnartowicz, 2004). The considerable variability in growth parameters within population was emphasized (Arbez, 1969).

A previous study showed that the response of silver fir's photosynthetic capacity to temperature was similar to that of a range of broadleaved species (Dreyer et al., 2001; Robakowski et al., 2002). Nevertheless, the acclimation potential of different provenances to short-term (days) increases in temperature was not studied at that time (Niinemets & Tenhunen, 1997). Moreover, a 2-year experiment in the nursery found that in general, the amplitude of responses of silver fir to changing irradiance (phenotypic plasticity) was smaller than that recorded with broadleaved species, but the potential occurrence of provenance effects has not yet been discussed (Robakowski et al., 2003). Intraspecific variation in silver fir was shown by many authors using isozymes and biometric parameters, but photosynthetic performance and physiological plasticity of different provenances have not been thoroughly investigated. The provenances characterized by different ecophysiological traits can show specific plasticity in response to light and temperature which can reflect, at least partially, their acclimation potential to the changing environment. In the context of this species decline and a recently observed improvement in its condition, it is of great significance to discover more about its intraspecific variation and plasticity, which can be done by determining the ecophysiological traits (e.g. photosynthetic capacity) of trees originating from different localities. These data can be helpful in the selection of *A. alba* provenances for silviculture.

The present study tested the hypothesis that seedlings originating from different localities and representing recognized provenances in Poland differ in growth, productivity (photosynthetic capacity and nitrogen use efficiency) and plasticity in response to changing irradiance and temperature. The first objective of the study was to examine the photosynthetic response of the five provenances acclimated to one of three temperatures (10, 25 and 35°C). The second objective was to check for intraspecific differences in the response of the same provenances to shade.

Materials and methods

Plant material

Seedlings of silver fir from five Polish provenances were used in the experiment (Table I, Figure 1). The provenances were selected from distant locations at a geographical and altitudinal scale with large local climate differences (Table II). The provenances were a mixture of seeds from 10 mother trees per provenance. The seeds from the strict reserve "Jata" (northern extremity of the *A. alba* range),

Table I. Provenances of *Abies alba* seedlings used in the study and sites where seeds were collected.

Location	Latitude, longitude	Altitude (m a.s.l.)	Exposition	Forest stand	Site type
“Siedlecka Upland”	51°54' N, 22°48' E	145	S	Strict reserve “Jata”: the northern limit of the <i>Abies alba</i> geographical range	Fresh mixed coniferous forest and fresh broadleaved forest
“Roztocze”	51°14' N, 23°19' E	345	S	Roztocze National Park, Reserve “Kamienna Góra”	Upland forest
“Beskid Sadecki”	49°31' N, 20°52' E	945	E and SE	Strict reserve “Labowiec”	Mixed mountain Forest
Sudety Mts	50°15' N, 16°45' E	520	S	Seed stand, in Forest Inspectorate “Miedzylesie”, the nursery in Miedzycgorze	Mixed mountain forest
		750	S	Mixed seeds from different stands	Mixed mountain forest

from Roztocze National Park (eastern limit of the natural range) and strict reserve “Labowiec” were sown in spring 1996 in a nursery in the Carpathians, near Nawojowa (49°31' N, 20°52' E). Those from Sudety provenances were sown in a nursery in the Sudety Mountains, near Miedzycgorze (50°15' N, 16°45' E). In both nurseries, seedlings were watered and grown for the first 3 years without fertilization, under moderate shade provided by a nearby spruce forest. During April 1999, they were put into

polyethylene rolls with soil from the nursery and transported to a nursery at Champenoux (48°44' N, 6°14' E), near Nancy, France. They were transplanted into 7 or 10 litre pots filled with a mixture of blond peat and sand (2/5 v/v).

Experimental design

In total, 500 seedlings were transported from Poland to the nursery at Champenoux: 200 seedlings in

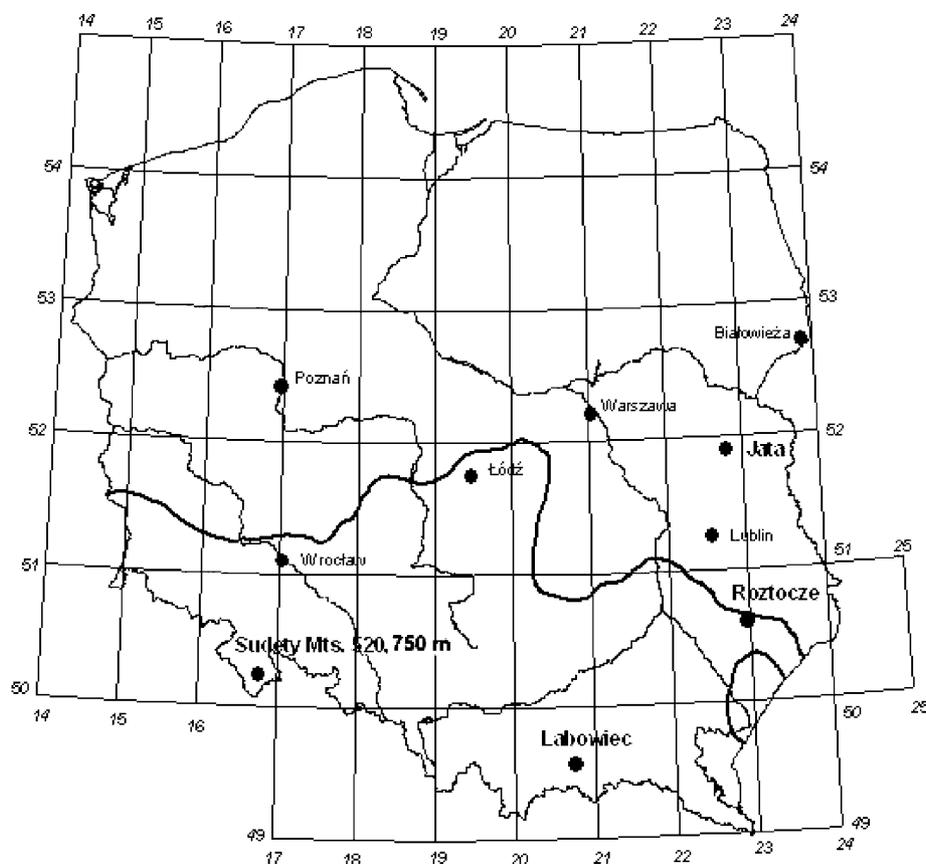


Figure 1. Map of Poland with the localities from which the seeds of *Abies alba* used in the experiment were collected (bold letters). The northern limit of the natural range of the species is shown with a thick line.

Table II. Climate parameters of the locations of provenances estimated based on the data from the closest climate stations.

Location	Altitude (m a.s.l.)	Temperature (°C) (monthly average)					Precipitation (mm)	
		Jan.	July	Annual average	Amplitude	Apr.–Sept.	Annual average	Apr.–Sept.
Siedlce Upland, strict reserve “Jata”	145	−4.4	18.4	7.2	22.8	14.3	546	187
“Roztocze”	345	–	–	6.9	–	13.7	673	–
Beskid Siedlecki, strict reserve “Labowiec”	945	–	–	6.9	–	10.2	950	–
Sudety Mts	520	−3.8	15.6	6.1	19.4	12.0	976	393
	750	–	–	5.1	–	11.0	1216	–

Note: for “Roztocze”, strict reserve “Labowiec” and “Sudety Mts 750” only the annual averages are given because of a lack of data.

10 litre pots were used in the outdoor shade response experiment in the nursery, and 200 seedlings in 7 litre pots were installed in a greenhouse before the temperature response experiment (75 were used in the climate chamber experiment). In the greenhouse, the mean daily temperature fluctuated between 19 and 32°C during the whole year, the relative air humidity (RH) remained at about 64% and the mean daily photosynthetic photon flux density (PPFD) values varied from 250 to 650 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Before starting the experiments four seedlings were collected per provenance (20 in total) during April 1999. They were oven-dried for 1 week at 65°C. Total seedling biomass, root biomass to total seedling biomass ratio (RMR) and shoot and needle biomass were measured. The remaining 105 seedlings were grown as a reserve.

Acclimation to temperature

In September 1999, 25 potted seedlings (five per provenance) were transferred to a climate chamber and acclimated under the following conditions: air temperature = 10°C, RH = 70% and PPFD = 250 $\mu\text{mol m}^{-2} \text{s}^{-1}$. A second set of 25 seedlings was acclimated to the temperature of 25°C and the third set to 35°C, while RH and PPFD were kept constant. The seedlings were exposed to each temperature for 1 week before measurements of gas exchange on current-year twigs, with a portable LiCor 6400 (LiCor, Nebraska, USA) under the following conditions in a leaf chamber: leaf temperature close to external, RH about 65% and PPFD at the saturating level of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Acclimation to shade

From April 1999 to September 2000, the seedlings were grown in 10 litre pots in the nursery of Champenoux, north-eastern France, under four different irradiance regimens: 100, 48, 18 or 8% of external irradiance, imposed with neutral shade nets.

Ten seedlings per provenance were acclimated during two full growing seasons to each irradiance treatment (200 seedlings in the whole experiment). During 1999 and 2000, they were fertilized at the beginning of May with 10 g $\text{l}_{\text{substrate}}^{-1}$ slow-release fertilizer Nutricote 100 13/13/13 N/P/K (supplemented with oligo-elements). Each seedling was watered to field capacity twice a day using drip irrigation. All measurements and chemical analyses were conducted during the second year of acclimation.

Shoot elongation and biomass

In the outdoor shade response experiment, the length of the terminal shoot and the length of the branches on the last whorl were measured after budset during September 2000 to compute an apical dominance ratio (ADR), i.e. the ratio between the length of the terminal shoot and the mean length of branches in the uppermost whorl. During September 2000, five seedlings were harvested per provenance and treatment, and the area and weight of 40 needles representing all age classes, as well as root, stem and needle biomass, were measured and used to compute whole seedling needle area and leaf mass to area ratio (LMA), RMR and leaf area to total seedling biomass ratio (LAR). Leaf projected area was computed with a Delta T Area Meter (Delta T, Hoddesdon, UK).

Gas exchange and nitrogen allocation to photosynthesis

In brief, from the end of June to the beginning of August 2000, five randomly selected seedlings (per provenance and per light treatment) from the shade experiment that had completed their extension growth were transferred to the laboratory. Gas exchange of twigs produced during the second growth season under the experimental conditions was recorded with a portable open gas-exchange system LiCor 6400. Estimates of maximum carboxylation rate (V_{cmax}) and maximal light-driven electron flow (J_{max}) were derived by fitting the

model of Farquhar et al. (1980) to the curves of carbon dioxide (CO₂) net assimilation in function of CO₂ substomatal concentration (A/C_i curves), as described in Dreyer et al. (2001). The values of V_{cmax} and J_{max} , and nitrogen content per leaf area were used to compute the fraction of total nitrogen allocated to the components of photosynthetic process: carboxylation (P_C), bioenergetics (P_B) and light harvesting complexes (P_L) (Hikosaka & Terashima, 1995, 1996; Niinemets & Tenhunen, 1997).

Nitrogen and chlorophyll content in needles

Needles collected from the top whorl of the seedlings used for gas exchange were dried and ground to a fine powder in a ball mortar. Samples from five seedlings per treatment per provenance were used for total nitrogen content analyses with the elemental analyser (Thermo-Quest NCS 2500) to obtain nitrogen and carbon content.

To analyse the chlorophyll content in needles, 50 mg of fresh needles from the top whorl of branches was macerated in 5 ml of 100% dimethylsulfoxide (DMSO) for 5 h at 65°C in a water bath until they became translucent. The absorbance of the extract was measured using a Hitachi 100–60 spectrophotometer at 666 nm and 649 nm. Chlorophyll a, b and total chlorophyll content were calculated using the formulae given by Barnes et al. (1992).

Statistical methods

Data from the temperature acclimation experiment were analysed using the linear regression model $y = ax + b$, where y = mean values of V_{cmax} , J_{max} , A_{max} or R_{d} ; a = slope; x = altitude of the seedlings origin; and b = intercept. Coefficients of determinations (R^2) with their probabilities were calculated to show the statistical significance of linear trends between the determined parameters and the altitudes of the seedlings' origin. To compare the provenances and their plasticity in response to different levels of shade, an analysis of covariance (ANCOVA) using the general linear model (GLM) was applied based on three variables: light, the continuous predictor variable; provenance, the categorical predictor variable; and measured parameters (total biomass, nitrogen concentration, etc.), the dependent variable. Before analysis, the values of fraction transmitted irradiance were ln-transformed. First, homogeneity of slopes design was used to test whether the continuous and categorical predictors (light and provenance) interacted in influencing the responses and, thus, whether the traditional ANCOVA design or the separate slope design was

appropriate for modelling the effects of predictors. When the interaction between the provenance and light was not statistically significant, the traditional ANCOVA was applied and followed by Tukey's a posteriori test ($p < 0.05$) to compare the provenances directly. If not, a separate slope design was applied and plasticity of the provenances in response to changing irradiance was analysed using Tukey's test at each level of irradiance. The prediction equations used in the study were:

(1) the homogeneity of slopes design:

$$Y = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_5 + b_6X_6 + b_7X_7 + b_8X_8 + b_9X_9$$

where Y = dependent variable; b_1 = the regression coefficient representing the influence of scores on the continuous predictor variable ("light") controlling for the influences of group membership on the categorical predictor variable ("provenance"); b_2, b_3, b_4, b_5 = regression coefficients representing the influences of group membership on the "provenance", controlling for the influence of scores on "light"; b_6, b_7, b_8, b_9 = regression coefficients representing the two-way interaction of "light" by "provenance";

(2) the traditional ANCOVA design:

$$Y = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_5$$

where b_1, b_2, b_3, b_4, b_5 = the regression coefficients as in (1);

(3) the separate slope design:

$$Y = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_5 + b_6X_6 + b_7X_7 + b_8X_8 + b_9X_9 + b_{10}X_{10}$$

where b_1, b_2, b_3, b_4, b_5 = regression coefficients representing the influences of group membership on the "provenance", controlling for the influence of scores on "light"; $b_6, b_7, b_8, b_9, b_{10}$ = regression coefficients giving the separate slopes for the regression of the outcome on "light" within each on "provenance", controlling for the main effect of "provenance". The detailed description of the mathematical models used in this study can be found in StatSoft (2004).

Ward's hierarchical clustering method was applied to group the provenances based on the mean values of determined parameters and the values of slopes in linear regression between ln (fraction transmitted irradiance + 1) and measured parameters. A clustering procedure was applied to the full data set, using the following procedure: data were grouped by categories (a: biomass data; b: leaf structure data; c: photosynthetic capacity data) and in each category the analysis comprised two steps (i) clustering based on the absolute means and (ii) clustering based on the plasticity of the traits with irradiance, i.e. the slopes of the linear regressions between the trait and

$\ln(\text{irradiance} + 1)$. The results are shown in Figure 3. In general, only the first knot of the resulting dendrogram was considered really significant owing to largest Ward index and the breakpoint in the curve on Ward indexes. All statistical analyses were done using Statistica 6.0.

Results

Response to temperature

At 25°C (Figure 2), the provenances from higher altitudes were characterized by higher values of V_{cmax} , J_{max} , maximum net CO₂ assimilation at ambient CO₂ concentration (35 Pa) and saturated level of PPFD (1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (A_{max}) and absolute values of (dark) respiration due to phosphorylative oxidation (R_{d}). Linear trends were determined between the elevation and all of these parameters. At 10°C, V_{cmax} and J_{max} reached very low values without any detectable difference among provenances. Similarly, A_{max} and R_{d} were rather low and very similar among provenances (Figure 2). At 35°C very drastic responses were observed in all parameters. The RuBP regeneration limited portion of the A/C_i curve was almost never reached and no correct estimate of J_{max} could be derived. V_{cmax} declined significantly in all provenances except for “Jata 145 m” a.s.l., and was not correlated with elevation. A_{max} was drastically reduced at 35°C compared with 25°C. No correlation could be detected between A_{max} and elevation. Finally, R_{d} displayed a severe increase, and surprisingly a negative correlation occurred between R_{d} and elevation. It must also be stressed that the plants displayed needle yellowing and needle shedding at this temperature, demonstrating that they suffered a severe heat shock.

Response to shade

Growth and biomass. Before the shading experiment, significant differences in total biomass were already recorded among provenances (largest values in the lower elevation “Sudety Mts” provenance, lowest in “Labowiec”, with very similar RMR, around 0.4, data not shown).

The length of the terminal shoot at the end of the second season was largest in the “Sudety Mts 520 m” and lowest in “Roztocze” (Table III). Although this length was independent of shade, the ADR depended on both provenance and irradiance. The highest values of ADR were reached in the “Sudety Mts 520” and the lowest in “Roztocze”. Total biomass at the end of the shading experiment displayed a large variability, with highly significant

effects of shade and provenance, and significant interactions between the two factors (Table III). The ranking of provenances remained the same as that recorded at the beginning of the experiments, despite the three-fold increase in biomass recorded in the full-sun individuals. “Sudety Mts 520” and “Jata” displayed the largest accumulated biomass. Irradiance-induced plasticity was limited in the smallest provenance (“Sudety Mts 750”) and much larger in provenances with important growth (“Jata 145”). The provenances with largest biomass also displayed the largest RMR, while no interprovenance variability was detected for LAR. These two parameters showed the expected response to shading (lower RMR and higher LAR in shade; Table III).

Needle structure. LMA responded positively to increasing irradiance, but no provenance-related difference was detected. In contrast, needle nitrogen concentration (N_{m}) displayed no irradiance response, but a very significant difference between provenances, with four of them (“Jata”, “Roztocze”, “Sudety Mts 750 m” and “Labowiec”) displaying much larger values than “Sudety Mts 520 m” (Table III). Total chlorophyll concentration in needles decreased severely with irradiance, and also differed among the provenances, with higher values in those with the lowest N_{m} (“Sudety Mts 520 m”). The chlorophyll a/b ratio did not significantly differ among the provenances.

Photosynthetic capacity. The provenances showed different photosynthetic capacities on a projected needle area basis and, as LMA was similar in all provenances, also on a needle biomass basis. The highest V_{cmax} and J_{max} were recorded in “Jata”, “Roztocze”, “Labowiec” and “Sudety Mts 750 m” (Table IV). R_{d} increased with irradiance, but also showed a significant provenance effect. R_{d} was highest in “Labowiec” and lowest in “Sudety Mts 750 m” (2.1 versus 1.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$), while the two provenances differed neither for LMA nor for N_{m} . Three groups of provenances were distinguished: “Roztocze 345”, “Sudety Mts 520” and “Labowiec” with the highest respiration, “Jata 145” with intermediate and “Sudety Mts 750” with the lowest rates.

P_{C} and P_{B} also showed a significant interprovenance variability, but no irradiance-induced change or irradiance–provenance interactions. P_{C} varied from 11 to 13% and P_{B} from 2.3 to 2.9%, i.e. the interprovenance variability remained small. Only “Sudety Mts 520” significantly differed from the

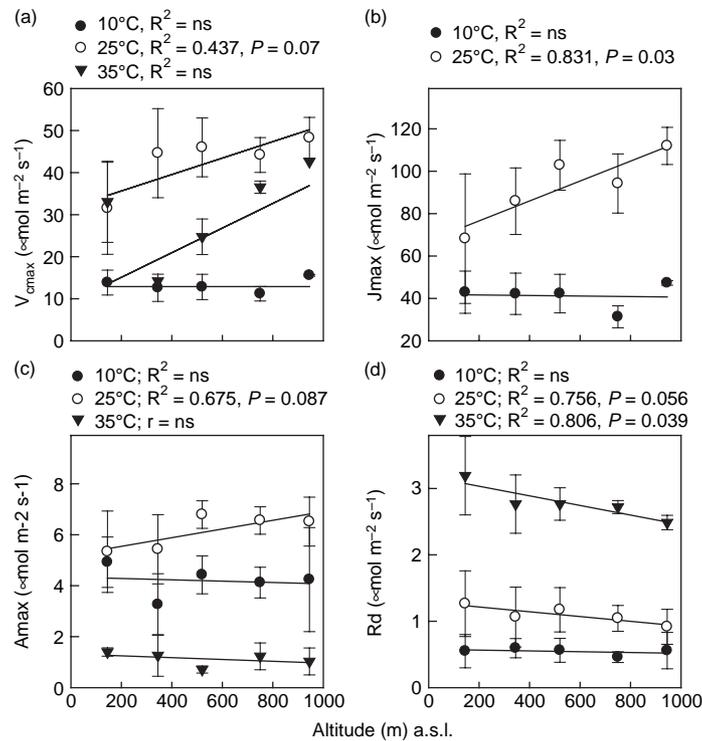


Figure 2. Correlation between the mean (\pm SD) values of: (a) maximum carboxylation rate (V_{cmax}), (b) maximum electron transport rate (J_{max}), (c) maximum net carbon dioxide assimilation rates (A_{max}), (d) dark respiration (R_d) and the altitudes of the seedlings' origin after weekly exposition to a temperature of 10, 25 and 35°C. Coefficients of determination (R^2) with the values of probabilities (p) are given.

other ones. The large allocation to photosynthesis did not result in a higher photosynthetic capacity, and only partially compensated the low N_m content recorded in the needles of this provenance. Allocation to light harvesting (P_L) decreased with increasing irradiance and varied substantially among provenances (from 6 to 11%).

Clustering of provenances

For the traits related to biomass (total biomass, RMR, LAR), a significant structure discriminated the provenances "Roztocze" and "Labowiec" from a group of two: "Jata" and "Sudety Mts 520". The "Sudety Mts 750" differed from all the other ones (Figure 3a). The clustering based on slopes of the relationships with irradiance showed no clear organization (data not shown). Needle structure led to a significant but different clustering: the provenance "Sudety Mts 520" differed from all other ones, owing mainly to low nitrogen and high chlorophyll concentrations (no provenance effect for LMA; Figure 3b1). The plasticity of these traits (Figure 3b2), photosynthetic capacity (Figure 3c) and the grouping of all parameters (Figure 3d) yielded a similar structure among provenances. "Sudety 520 and 750" differed from "Jata" and differed even more from a group of two provenances, "Roztocze" and "Labowiec". The analysis

of plasticity in photosynthetic traits produced no really significant (data not shown). Finally, the plasticity of all traits allowed segregation of the two provenances "Jata" and "Roztocze", but not organization of the remaining ones (data not shown).

Discussion

Photosynthetic performance showed some diversity among Polish provenances of *A. alba* at 25°C. In particular, J_{max} increased linearly with elevation of the provenance. This relationship between the altitude of seedlings' origin and photosynthetic capacity was less pronounced than in *P. abies* (Oleksyn et al., 1998). This diversity was no longer visible at 10°C. The abrupt decrease in photosynthetic capacity after 1 week at 35°C, followed by needle yellowing and shedding, resulted from severe heat stress and proved that this species was unable to acclimate to such high temperature. In an earlier study (Robakowski et al., 2002), it was suggested that the thermal responses of photosynthetic capacity of silver fir were similar to those obtained with potted seedlings from a range of broadleaved species, but remained in the lower range, close to those of the shade-tolerant *Acer pseudoplatanus* L. and *Fagus sylvatica* L. (Dreyer et al., 2001; Robakowski et al., 2002). It can be stated that in silver fir, which is one of the most shade-tolerant European tree

Table III. Mean values (\pm SD) of length of terminal shoot, apical dominance ratio (ADR), total biomass, root mass ratio (RMR), nitrogen (N_m) and chlorophyll concentrations of *Abies alba* seedlings from five provenances submitted during two years to four levels of irradiance.

Provenance (m a.s.l.)	Average provenance value	Fraction transmitted irradiance			
		0.08	0.18	0.48	1.00
	Terminal shoot (mm)				
Jata 145	76 \pm 20a	61 \pm 13a	78 \pm 14a	91 \pm 17ab	75 \pm 21a
Roztocze 345	71 \pm 20a	48 \pm 16a	86 \pm 14a	72 \pm 9a	74 \pm 18a
Sudety Mts 520	97 \pm 27b	82 \pm 8b	120 \pm 26b	116 \pm 20b	77 \pm 20a
Sudety Mts 750	79 \pm 25a	51 \pm 14a	93 \pm 17b	85 \pm 24b	87 \pm 20a
Labowiec 945	73 \pm 24a	54 \pm 11a	92 \pm 22b	75 \pm 22b	75 \pm 24a
<i>p</i> -Values	Provenance $p < 0.001$, Treatment $p = 0.121$, Interaction $P \times T p = 0.037$				
	ADR				
Jata 145	0.686 \pm 0.142ab	0.592 \pm 0.120	0.672 \pm 0.105	0.784 \pm 0.105	0.695 \pm 0.160
Roztocze 345	0.614 \pm 0.129a	0.472 \pm 0.104	0.677 \pm 0.074	0.609 \pm 0.072	0.674 \pm 0.132
Sudety Mts 520	0.762 \pm 0.152b	0.654 \pm 0.118	0.860 \pm 0.147	0.864 \pm 0.119	0.694 \pm 0.102
Sudety Mts 750	0.689 \pm 0.150ab	0.525 \pm 0.097	0.774 \pm 0.115	0.717 \pm 0.153	0.737 \pm 0.078
Labowiec 945	0.662 \pm 0.155a	0.567 \pm 0.121	0.737 \pm 0.136	0.660 \pm 0.128	0.695 \pm 0.183
<i>p</i> -Values	Provenance $p = 0.003$, Treatment $p = 0.006$, Interaction $P \times T p = 0.339$				
	Total biomass (g)				
Jata 145	82 \pm 47a	16 \pm 2ab	57 \pm 22a	141 \pm 25a	105 \pm 4ab
Roztocze 345	58 \pm 32b	17 \pm 2ab	43 \pm 8a	68 \pm 16b	92 \pm 25ab
Sudety Mts 520	82 \pm 23a	43 \pm 6c	69 \pm 7a	94 \pm 17ab	113 \pm 10a
Sudety Mts 750	51 \pm 20b	26 \pm 6ab	47 \pm 16a	58 \pm 15b	73 \pm 3b
Labowiec 945	55 \pm 35b	17 \pm 5a	48 \pm 16a	74 \pm 29b	89 \pm 26ab
<i>p</i> -Values	Provenance $p < 0.001$, Treatment $p < 0.001$, Interaction $P \times T p < 0.001$				
	RMR				
Jata 145	0.394 \pm 0.098abd	0.255 \pm 0.002ab	0.341 \pm 0.019ab	0.431 \pm 0.043ab	0.523 \pm 0.038ab
Roztocze 345	0.368 \pm 0.096bc	0.227 \pm 0.019b	0.332 \pm 0.023ab	0.394 \pm 0.031ab	0.484 \pm 0.023ab
Sudety Mts 520	0.416 \pm 0.076d	0.301 \pm 0.010a	0.389 \pm 0.033a	0.447 \pm 0.019a	0.503 \pm 0.030ab
Sudety Mts 750	0.342 \pm 0.09c	0.299 \pm 0.009a	0.314 \pm 0.033b	0.373 \pm 0.041b	0.397 \pm 0.026c
Labowiec 945	0.363 \pm 0.077abc	0.257 \pm 0.017ab	0.372 \pm 0.034ab	0.401 \pm 0.018ab	0.449 \pm 0.026ac
<i>p</i> -Values	Provenance $p < 0.001$, Treatment $p < 0.001$, Interaction $P \times T p < 0.001$				
	LAR ($m^2 kg^{-1}$)				
Jata 145	1.671 \pm 0.725	3.050 \pm 0.085ab	1.848 \pm 0.066ab	1.284 \pm 0.096a	0.901 \pm 0.169a
Roztocze 345	1.630 \pm 0.768	2.956 \pm 0.322a	1.657 \pm 0.056ab	1.228 \pm 0.053a	0.951 \pm 0.055a
Sudety Mts 520	1.717 \pm 0.631	2.836 \pm 0.205ab	1.745 \pm 0.158ab	1.341 \pm 0.074a	1.171 \pm 0.081a
Sudety Mts 750	1.911 \pm 0.346	2.317 \pm 0.166b	2.063 \pm 0.193b	1.705 \pm 0.282b	1.521 \pm 0.111b
Labowiec 945	1.702 \pm 0.720	2.755 \pm 0.158ab	1.581 \pm 0.159a	1.219 \pm 0.059a	0.992 \pm 0.043a
<i>p</i> -Values	Provenance $p = 0.667$, Treatment $p < 0.001$, Interaction $P \times T p < 0.001$				
	LMA ($g m^{-2}$)				
Jata 145	156 \pm 29	111 \pm 1a	140 \pm 5a	174 \pm 4a	190 \pm 7a
Roztocze 345	151 \pm 28	112 \pm 1a	134 \pm 7a	165 \pm 13a	183 \pm 4a
Sudety Mts 520	154 \pm 28	114 \pm 5a	140 \pm 5a	168 \pm 16a	186 \pm 5a
Sudety Mts 750	157 \pm 20	136 \pm 3b	149 \pm 19a	165 \pm 10a	181 \pm 5a
Labowiec 945	150 \pm 27	115 \pm 5a	147 \pm 4a	164 \pm 6a	184 \pm 9a
<i>p</i> -Values	Provenance $p = 0.240$, Treatment $p < 0.001$, Interaction $P \times T p < 0.001$				
	N_m ($mg g^{-1}$)				
Jata 145	22.2 \pm 2.2a	20.7 \pm 0.6	21.5 \pm 2.2	22.5 \pm 2.3	24.0 \pm 1.4
Roztocze 345	22.8 \pm 1.9a	21.8 \pm 2.9	23.6 \pm 1.4	23.5 \pm 1.4	22.3 \pm 0.8
Sudety Mts 520	13.9 \pm 2.5b	14.3 \pm 2.6	15.2 \pm 2.8	13.1 \pm 1.1	13.3 \pm 2.6
Sudety Mts 750	21.7 \pm 1.8a	20.4 \pm 1.9	21.0 \pm 1.5	22.7 \pm 1.5	22.8 \pm 1.4
Labowiec 945	21.6 \pm 2.2a	21.5 \pm 1.8	19.8 \pm 1.0	23.0 \pm 1.9	22.2 \pm 2.4
<i>p</i> -Values	Provenance $p < 0.001$, Treatment $p = 0.189$, Interaction $P \times T p = 0.096$				
	Chl ($mg g^{-1}$)				
Jata 145	1.89 \pm 0.506a	2.67 \pm 0.536a	1.99 \pm 0.147a	1.82 \pm 0.175a	1.32 \pm 0.154a
Roztocze 345	2.11 \pm 0.368a	2.55 \pm 0.211a	2.24 \pm 0.091ab	2.06 \pm 0.167ab	1.69 \pm 0.264a
Sudety Mts 520	2.66 \pm 1.096b	4.41 \pm 0.047b	3.02 \pm 0.217b	2.16 \pm 0.306ab	1.40 \pm 0.083a
Sudety Mts 750	1.90 \pm 0.313a	2.34 \pm 0.069a	2.01 \pm 0.172a	1.63 \pm 0.215a	1.61 \pm 0.115a
Labowiec 945	1.92 \pm 0.363a	2.33 \pm 0.202a	1.89 \pm 0.145a	1.89 \pm 0.241a	1.46 \pm 0.60a
<i>p</i> -values	Provenance $p < 0.014$, Treatment $p < 0.001$, Interaction $P \times T p < 0.001$				

ANCOVA (according to general linear models) was used to analyse the effects of provenance, irradiance and the interaction between provenance and irradiance [number of replicates (n) = 5]. The effects were considered statistically significant at $p < 0.05$. p is the values of probabilities obtained from ANCOVA for provenance, treatment and interaction between provenance and treatment effects. The same letters indicate a lack of statistically significant differences between the provenances and, when the interaction was statistically significant, between the provenances within irradiance treatment according to Tukey's a posteriori test ($p < 0.05$).

Table IV. Mean values (\pm SD) of maximal carboxylation rate (V_{cmax}), maximal electron transport rate (J_{max}), dark respiration (R_d), relative nitrogen allocation to carboxylation (P_C) to bioenergetics (P_B), to light harvesting complexes (P_L), nitrogen and total chlorophyll concentration in needles of the seedlings of *Abies alba* acclimated to four levels of irradiance ($n=5$).

Provenance (m a.s.l.)	V_{cmax} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Fraction transmitted irradiance			
		0.08	0.18	0.48	1.00
Jata 145	53 \pm 12a	34 \pm 3	49 \pm 6	59 \pm 6	65 \pm 2
Roztocze 345	49 \pm 12a	34 \pm 6	45 \pm 7	52 \pm 8	61 \pm 7
Sudety Mts 520	36 \pm 9b	24 \pm 2	36 \pm 8	37 \pm 4	44 \pm 7
Sudety Mts 750	47 \pm 11a	35 \pm 5	45 \pm 6	46 \pm 6	61 \pm 9
Labowiec 945	45 \pm 9a	36 \pm 5	45 \pm 4	47 \pm 7	54 \pm 8
<i>p</i> -Values	Provenance $p < 0.001$, Treatment $p < 0.001$, Interaction $P \times T$ $p = 0.252$				
	J_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)				
Jata 145	117 \pm 34a	66 \pm 2ab	101 \pm 19a	137 \pm 18a	151 \pm 18a
Roztocze 345	110 \pm 27ac	72 \pm 8ab	105 \pm 14a	122 \pm 19a	133 \pm 19a
Sudety Mts 520	78 \pm 19b	56 \pm 4b	78 \pm 18a	79 \pm 9b	94 \pm 9b
Sudety Mts 750	99 \pm 26c	67 \pm 9ab	92 \pm 10a	98 \pm 11ab	137 \pm 11a
Labowiec 945	100 \pm 21ac	76 \pm 9a	98 \pm 7a	111 \pm 16ab	123 \pm 16ab
<i>p</i> -Values	Provenance $p < 0.001$, Treatment $p < 0.001$, Interaction $P \times T$ $p < 0.001$				
	R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)				
Jata 145	1.832 \pm 0.715ab	0.999 \pm 0.084a	1.380 \pm 0.299a	2.518 \pm 0.588a	2.303 \pm 0.380ab
Roztocze 345	2.119 \pm 0.765a	1.121 \pm 0.260ab	1.979 \pm 0.117ab	2.353 \pm 0.528a	2.793 \pm 0.666a
Sudety Mts 520	1.803 \pm 0.397a	1.390 \pm 0.186a	1.515 \pm 0.184a	2.081 \pm 0.298a	2.143 \pm 0.184ab
Sudety Mts 750	1.371 \pm 0.381b	0.866 \pm 0.145b	1.623 \pm 0.347ab	1.267 \pm 0.183b	1.424 \pm 0.262b
Labowiec 945	2.142 \pm 0.783a	1.121 \pm 0.223ab	2.352 \pm 0.636b	2.560 \pm 0.210a	2.793 \pm 0.386a
<i>p</i> -Values	Provenance $p < 0.001$, Treatment $p < 0.001$, Interaction $P \times T$ $p < 0.001$				
	P_C				
Jata 145	0.118 \pm 0.011ab	0.116 \pm 0.011	0.125 \pm 0.014	0.117 \pm 0.002	0.111 \pm 0.007
Roztocze 345	0.109 \pm 0.016a	0.107 \pm 0.012	0.109 \pm 0.017	0.103 \pm 0.018	0.116 \pm 0.014
Sudety Mts 520	0.131 \pm 0.022b	0.120 \pm 0.028	0.130 \pm 0.016	0.131 \pm 0.014	0.141 \pm 0.023
Sudety Mts 750	0.109 \pm 0.022a	0.098 \pm 0.015	0.117 \pm 0.027	0.095 \pm 0.009	0.116 \pm 0.016
Labowiec 945	0.109 \pm 0.018a	0.116 \pm 0.013	0.118 \pm 0.006	0.096 \pm 0.007	0.105 \pm 0.027
<i>p</i> -Values	Provenance $p = 0.002$, Treatment $p = 0.810$, Interaction $P \times T$ $p = 0.319$				
	P_B				
Jata 145	0.026 \pm 0.003ab	0.023 \pm 0.001	0.027 \pm 0.004	0.028 \pm 0.002	0.026 \pm 0.001
Roztocze 345	0.025 \pm 0.004a	0.024 \pm 0.001	0.026 \pm 0.004	0.025 \pm 0.004	0.026 \pm 0.003
Sudety Mts 520	0.029 \pm 0.004b	0.028 \pm 0.005	0.029 \pm 0.004	0.029 \pm 0.002	0.031 \pm 0.006
Sudety Mts 750	0.023 \pm 0.005a	0.019 \pm 0.003	0.024 \pm 0.005	0.021 \pm 0.002	0.027 \pm 0.003
Labowiec 945	0.025 \pm 0.003a	0.025 \pm 0.002	0.027 \pm 0.001	0.023 \pm 0.002	0.024 \pm 0.006
<i>p</i> -Values	Provenance $p = 0.0002$, Treatment $p = 0.092$, Interaction $P \times T$ $p = 0.669$				
	P_L				
Jata 145	0.059 \pm 0.011a	0.073 \pm 0.008a	0.062 \pm 0.006a	0.058 \pm 0.005a	0.045 \pm 0.001a
Roztocze 345	0.061 \pm 0.008a	0.070 \pm 0.004a	0.063 \pm 0.003a	0.058 \pm 0.005a	0.054 \pm 0.007a
Sudety Mts 520	0.106 \pm 0.035b	0.157 \pm 0.034b	0.110 \pm 0.014b	0.094 \pm 0.006b	0.072 \pm 0.009b
Sudety Mts 750	0.057 \pm 0.008a	0.065 \pm 0.007a	0.061 \pm 0.005a	0.049 \pm 0.006a	0.050 \pm 0.004a
Labowiec 945	0.063 \pm 0.018a	0.080 \pm 0.022a	0.065 \pm 0.001a	0.055 \pm 0.001a	0.049 \pm 0.007a
<i>p</i> -Values	Provenance $p = 0.004$, Treatment $p < 0.001$, Interaction $P \times T$ $p < 0.001$				

Note: for further explanations see Table III.

species, photosynthesis is more sensitive to high temperatures than in the less shade-tolerant trees. A temperature of 35°C often occurs above ground in the summer and can damage young firs growing in the open. For this reason, seedlings should be planted under mature trees canopy or in gaps where climatic conditions are characterized by lower amplitudes of air temperature.

In the nursery experiment, provenances differed significantly in morphological and physiological traits. Such differences in morphological traits may

be ascribed to differences in sapling size (ontogenetic effect) or to a direct effect of provenance or shade (true plasticity). Indeed, RMR and leaf area were positively correlated with sapling biomass, and LAR negatively (Robakowski et al., 2003). The main features of plasticity in response to irradiance were substantial increases in biomass production, photosynthetic capacity and LMA with increasing irradiance, and small or non-significant changes in N_m , and in allocation of nitrogen to photosynthetic processes within needles.

Cluster analysis based on all measured parameters yielded a well-defined grouping of provenances (Figure 3d) that was consistent with the mountain massifs of the seed origin. The provenances from the Sudety Mountains largely differed from the Carpathian and “Jata” not only in growth and biomass (Gunia, 1986), but also in photosynthetic performance. Therefore, this study was unable to detect a consistent variability in overall responses to temperature or shading among the different provenances, and could not provide evidence for any ecotype with respect to temperature or solar irradiance responses. However, based on the results, it cannot be excluded that ecotypic variation may be shown with plant material originating from geographically more contrasting regions and a clinal variation using seeds from several altitudes and one mountain slope. The provenances used in this study originated from different localities and altitudes, but were not selected along any constant ecological gradient. This makes it difficult to attribute the interprovenance differences to altitude, latitude or geographical isolation. Sagnard et al. (2002), consistently with the present results, did not find any geographical pattern of overall allozyme differentiation among scattered silver fir populations from the south-western Alps. A closer examination of the performance parameters yields the following features for the different provenances.

The provenance “Sudety Mts 520” was characterized by:

- high biomass productivity, with a rather large investment into root biomass
- a low level of N_m in needles and a high level of chlorophyll (both expressed on a needle mass basis)
- rather low photosynthetic capacity per unit needle area, the low N_m being partially compensated by a slightly larger allocation of needle nitrogen to photosynthesis.

Group 2 comprised the low-elevation provenances (“Jata” and “Roztocze”), which had:

- large growth with lower allocation to roots
- high N_m and low chlorophyll concentration in needles
- high photosynthetic capacity with a smaller allocation of nitrogen to photosynthesis.

Group 3 comprised the high-elevation provenances (Sudety Mts 750 m” and “Labowiec”), characterized by:

- the lowest biomass accumulation; low investment into roots
- high N_m and low chlorophyll concentration
- intermediate levels of photosynthesis and intermediate investment of nitrogen into photosynthesis.

The morphological and physiological differentiation among the populations found in this study seems to contradict the hypothesis about low levels of diversity of silver fir in north-eastern Europe, consistent with the results obtained by Szymura (2003).

The studies in *P. abies* seedlings (Oleksyn et al., 1998) showed that high-altitude provenances had higher N_m and, consequently, larger photosynthetic capacities, together with a lower total biomass increment than lower elevation ones. Although N_m effectively discriminated the provenances in this case, no apparent relationship with altitude and microclimate was found. Moreover, the differences in N_m were to some extent modulated by changes in nitrogen allocation to photosynthesis, which compensated at least partly for the difference in N_m . A larger photosynthetic capacity, particularly under high irradiance, in the provenances “Labowiec”, “Sudety Mts 750” and “Jata” compared with the other ones, may be considered as an adaptation to light environment (Colom et al., 2003). It was therefore impossible to reach conclusions about the occurrence of altitudinal ecotypes of firs based on the results of this experiment. This lack of significant relationships between the altitude, microclimate conditions and silver fir growth and performance, despite the occurrence of significant differences in growth and photosynthetic parameters among provenances, may result from a high genetic diversity within populations, which was about 80% in Carpathian and Sudety provenances (Mejnartowicz, 2004). This may partly mask interpopulation variation. In addition, the pollen and seeds of *A. alba* are relatively heavy, which may significantly reduce its ecotypic and clinal variation compared with the other wind-pollinated trees (e.g. *P. abies*). Furthermore, a large variability in adaptive traits was found within populations from the south-western Alps, indicating that selective forces operate in isolated and scattered fir populations at the microgeographical level (Sagnard et al., 2002).

In conclusion, the results indicate that the ecophysiological plasticity of *A. alba* seedlings in response to temperature and light differed among the investigated provenances. Evidence was provided for the existence of functional variation

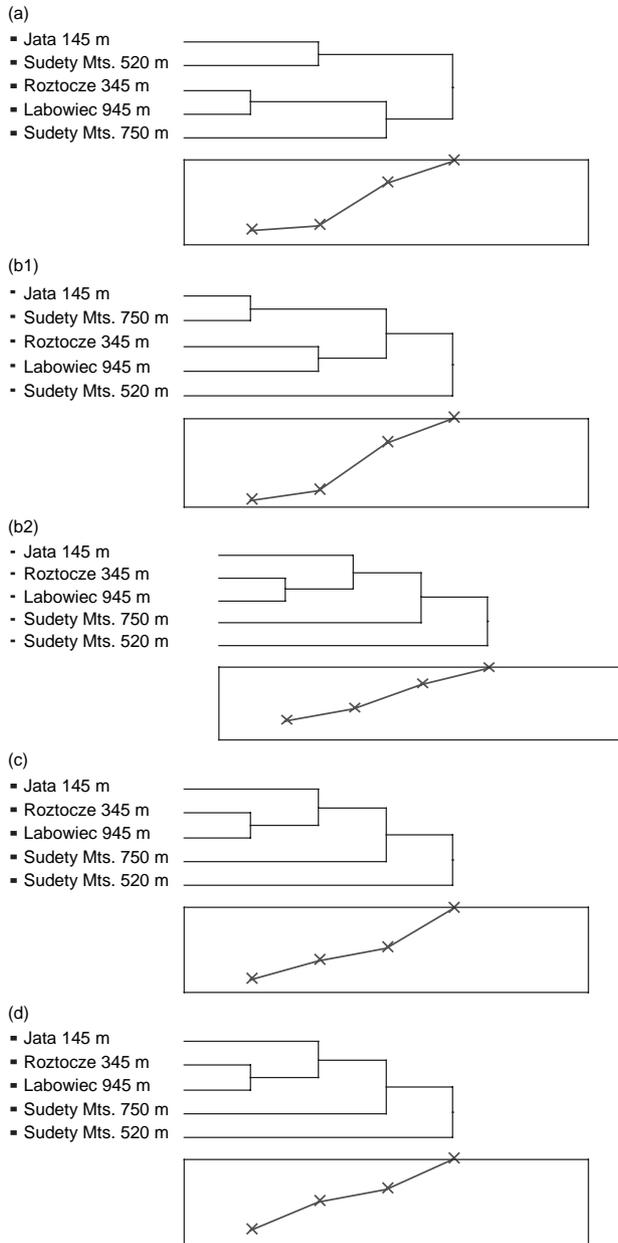


Figure 3. Cluster dendrogram of provenances of silver fir. The following parameters were used as clustering variables: (a) mean values of seedling biomass, root to total biomass ratio (RMR), leaf area to total biomass ratio (LMR); (b1) mean values of leaf mass to area ratio (LMA), nitrogen concentration (N_m), total chlorophyll concentration in needle; (b2) slopes of linear regression lines between $\ln(\text{irradiance} + 1)$ and LMA, N_m , total chlorophyll; (c) mean values of maximal carboxylation rate (V_{cmax}), maximal electron transport rate (J_{max}), (dark) respiration due to phosphorylative oxidation (R_d), nitrogen fraction allocated to bioenergetics (P_B), nitrogen fraction allocated to carboxylation (P_C), nitrogen fraction allocated to light harvesting complexes (P_L); (d) mean values of all the parameters. The distance graph beneath the dendrogram presents points for each cluster. The distance between points represents the distance between the clusters.

among these provenances, which may be important for silviculture. It may be suggested that large

within-population variation, as well as interprovenance, non-ordered genetic and phenotypic variability, is typical for silver fir, which has a discontinuous area of distribution, made up of many isolated populations. Further experiments with more provenances are necessary to determine the ecological properties of silver fir ecotypes and preserve ecotypic diversity, which is essential for the adaptation of the species to changing environmental conditions.

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