



# How geographic and climatic factors affect the adaptation of Douglas-fir provenances to the temperate continental climate zone in Europe

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## Abstract

The contribution of Douglas-fir (Df) to European forests is likely to increase as the species is a potential adaptation option to climate change. In this study, we investigated growth and survival of Df seed sources to fill a knowledge gap regarding recommendations for the future use of Df provenances in Poland. Our experimental test site represents the most continental climate among all Df trials installed in the IUFRO 1966–67 test series in Europe. At this unique single site, we evaluated the performance of 46 Df provenances from North America, and nine local landraces of unknown origin. Repeated measurements of tree diameter, height, and volume were analysed, to age 48, representing integrated responses to geographic and climatic conditions. Significant variation in survival and productivity-related traits were found, with the interior Df provenances performing best, in contrast to previous European reports. The higher survivability and volume of the interior provenances resulted from their superior frost resistance. The low precipitation seasonality at the location of seed origin provided an additional advantage to the trees at the test site. Geographic and climatic factors of seed origin explained most of the variation in productivity (77 and 64%, respectively). The tested landraces exhibited diverse performance, implying that naturalized local seed sources in Poland need improvement and perhaps enrichment with new genetic material from North America, while considering geography and climate. Assisted migration programs should consider the limitations imposed by both frost and drought events in guiding future Df selections for continental climates. Further field testing, early greenhouse screening and DNA testing are also recommended.

**Keywords** Douglas-fir · Provenance trial · Adaptation · Productivity · Climatic factors · Generalized additive models · Landrace

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## Introduction

With ongoing climate change occurring at a speed far exceeding the natural adaptive abilities of forest trees (Davis and Shaw 2001; Nathan et al. 2011), forestry faces new challenges in the context of afforestation and possible changes in species composition of forest stands (Allen et al. 2010). These challenges put the long-term provenance experiments carried out around the world in a new light, providing new information to support matching provenances with projected future climates for assisted migration programs (Wang et al. 2006, 2010; Rousi et al. 2012).

The growth and survival of trees at specific sites or regions depend on their adaptive capacity and plasticity (Kijowska-Oberc et al. 2020). Population-specific responses to climate and other factors are usually examined in common

garden experiments, where the adaptability is assessed on the basis of survival rate and the phenotypic traits of primary interest for forestry, such as tree height and diameter. Historically, the main objective of such studies was to evaluate populations within a species and select those which are best adapted, productive and resistant to biotic and abiotic stresses (White et al. 2007). However, many provenance tests have been revisited to assess these populations' adaptive ability to specific climatic conditions and climate change in particular (Matyas 1994; Schmidting 1994; Andalo et al. 2005; Aitken et al. 2008; Chakraborty et al. 2015, 2016). Long-term provenance experiments are best suited to achieve this goal, combined with a rapidly changing climate, the empirical results available from these transplant studies can support successful programs geared at assisted migration or assisted colonization of introduced forest tree species (moving planting material outside their natural range) (Aitken and Whitlock 2013).

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Df), a conifer native to North America, is a prime example of a tree species of global importance to forestry. With the two major geographic varieties – the coastal or green type *P. menziesii* var. *menziesii*, and the interior, Rocky Mountain, or blue type *P. menziesii* var. *glauca* – Df spans an enormous geographic range in western North America (Hermann and Lavender 1999). Due to its superior productivity, wood quality, and high market value (Krakowski and Stoehr 2009), Df has been introduced into many countries around the world (Chakraborty et al. 2015) including those in Europe where the species has been planted since the early nineteenth century (Lavender and Hermann 2014; van Loo and Dobrowolska 2020). At present, Df plantations occupy more than 823,534 hectares in 35 European countries, which accounts for 0.4% of the European forest area (Bastien et al. 2013; Konnert and Bastien 2019). This area represents the largest planting of any non-native forest-forming tree species in several European countries, including Germany, France and Poland (Barzdajn 2013; van Loo and Dobrowolska 2020).

Due to the importance of Df for forestry, the genetic variation in this species has been investigated in numerous provenance trials in North America, Europe and elsewhere. Having evolved in highly heterogeneous environments, Df exhibits large intraspecific variation in many phenotypic traits (St Clair and Howe 2007; Krakowski and Stoehr 2009; Leites et al. 2012; Rehfeldt et al. 2014; Bansal et al. 2015; St Clair et al. 2020). Thus, the response to specific climatic conditions, when moved to new regions, may vary among populations. To obtain a better understanding of the potential of this species, in 1966–67, the International Union of Forest Research Organizations (IUFRO) carried out a systematic and representative collection of seed, covering the entire natural range of the species. In this experiment, 182 provenances of *Pseudotsuga* were tested throughout 36

countries worldwide (Kleinschmit and Bastien 1992; Bastien et al. 2013; Konnert and Bastien 2019), including Poland, where over 100 provenances have been studied (Mejnartowicz 1976; Burzyński 1990).

Introduction of Df to Poland (within its current borders), as in many other European countries (e.g. Germany, the Netherlands), began long before these IUFRO collections were made and the first systematic provenance trials were established (Barzdajn 2013). Df was introduced to Poland in 1830 (Burzyński 1990; Kleinschmit and Bastien 1992; Chylarecki 2004) with a large increase in area planted to Df from 1895–1945, thanks to the activities of prof. Schwappach, and following the encouraging results of those introductions (Barzdajn 2013). Those early plantings of Df, resulted in the existence of well-adapted mature stands today (Chylarecki 2004), although the parental origin of these stands remains unclear. These long established stands have now naturalized to the Polish landscape, forming local landraces (Zobel and Talbert 1984), making them a potential ideal source of seed for future use.

Early observations of provenance trials from the 1966–67 IUFRO Df collection established in Poland, enriched by progeny from the populations previously introduced to Poland (now local landraces), has allowed for early recognition of both frost resistance and survival rate in selected provenances (Burzyński 1990). The early results of height growth from 120 experimental plots established throughout Europe, including the Polish trials, were also included in the retrospective study on Df adaptation potential (exclusively IUFRO seed collections) under the current and projected future climates in Europe (Isaac-Renton et al. 2014). However, the provenance performance models developed had a weaker predictive power for Central Europe (referred to as Eastern Europe in Isaac-Renton et al. (2014)), with a more continental climate (Poland), than for most of the other sites studied (Isaac-Renton et al. 2014). The lack of sufficiently accurate prediction power of these models, in terms of the growth potential of specific Df provenances at more continental sites, and the fact that the relative performance of provenances may vary through time, prompted the undertaking of more detailed research focused exclusively on Polish conditions.

Df is considered a 'winner species' for Central Europe according to species distribution models under projected climate change scenarios (Dyderski et al. 2018) and its contribution to forests in Europe is likely to increase in the future. Df may be considered as an alternative to some native, highly productive conifer species (e.g. Norway spruce), whose decline is observed in many regions in Central Europe. The importance of Df for Polish forestry is shown through its inclusion in the "Program of conserving forest genetic resources and breeding of trees in Poland for the years 2011–2035" (Chałupka et al. 2011). However, there

are still no official recommendations regarding the use of Df provenances in Poland. Furthermore, few attempts have been made to relate the climatic conditions of the seed sources to those of the proposed deployment areas, or to test for local adaptation and effects of provenance transfers, especially to continental climatic conditions (Mejnartowicz 1976; Burzyński 1990).

The aim of this study was to analyse the effect of geographical location and climatic conditions of Df origin, on its survival, growth rate and productivity in a long-term provenance trial established in eastern Poland. This trial represents the most continental climatic conditions among all of the lowland trial sites from the IUFRO 1966–67 Df trial series installed in Europe. Seedlots from the local landraces were also included in this eastern Polish trial to evaluate their productivity and usefulness as potential seed sources for the country. Results of this study may support decisions regarding seed transfer and limitations to assisted migration of Df in future forest practices.

## Materials and methods

### Provenance trial

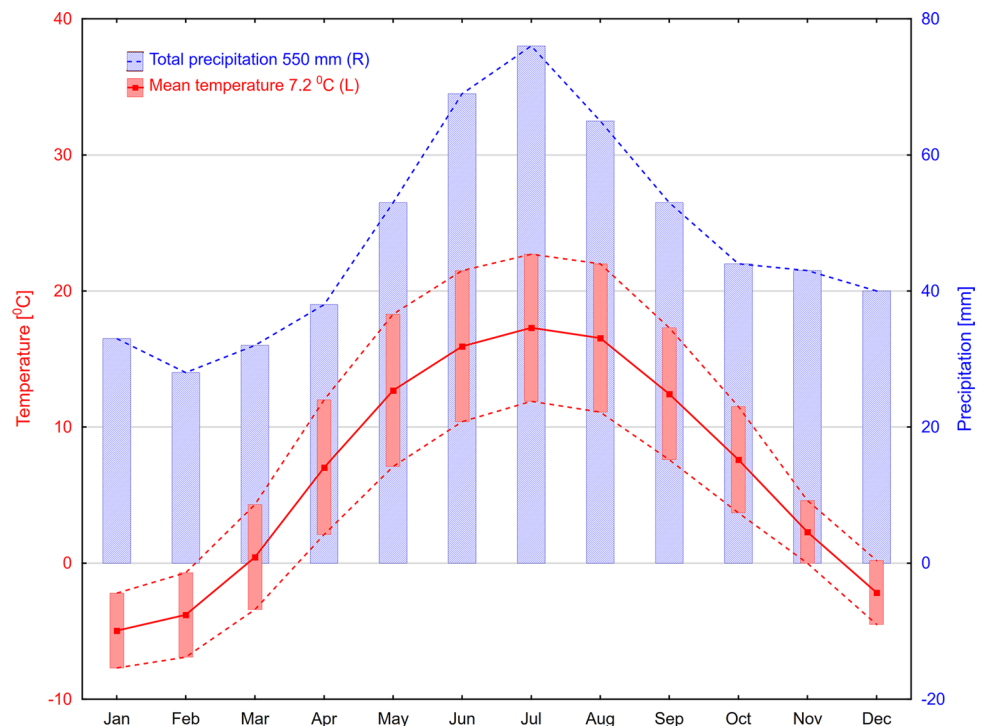
The experimental area of the eastern Polish trial (Rudka) site was established in 1974 in the Rudka Forest District. This area is located in the lowland part of Poland (52°41'33"N, 22°42'32"E), with a prevailing temperate

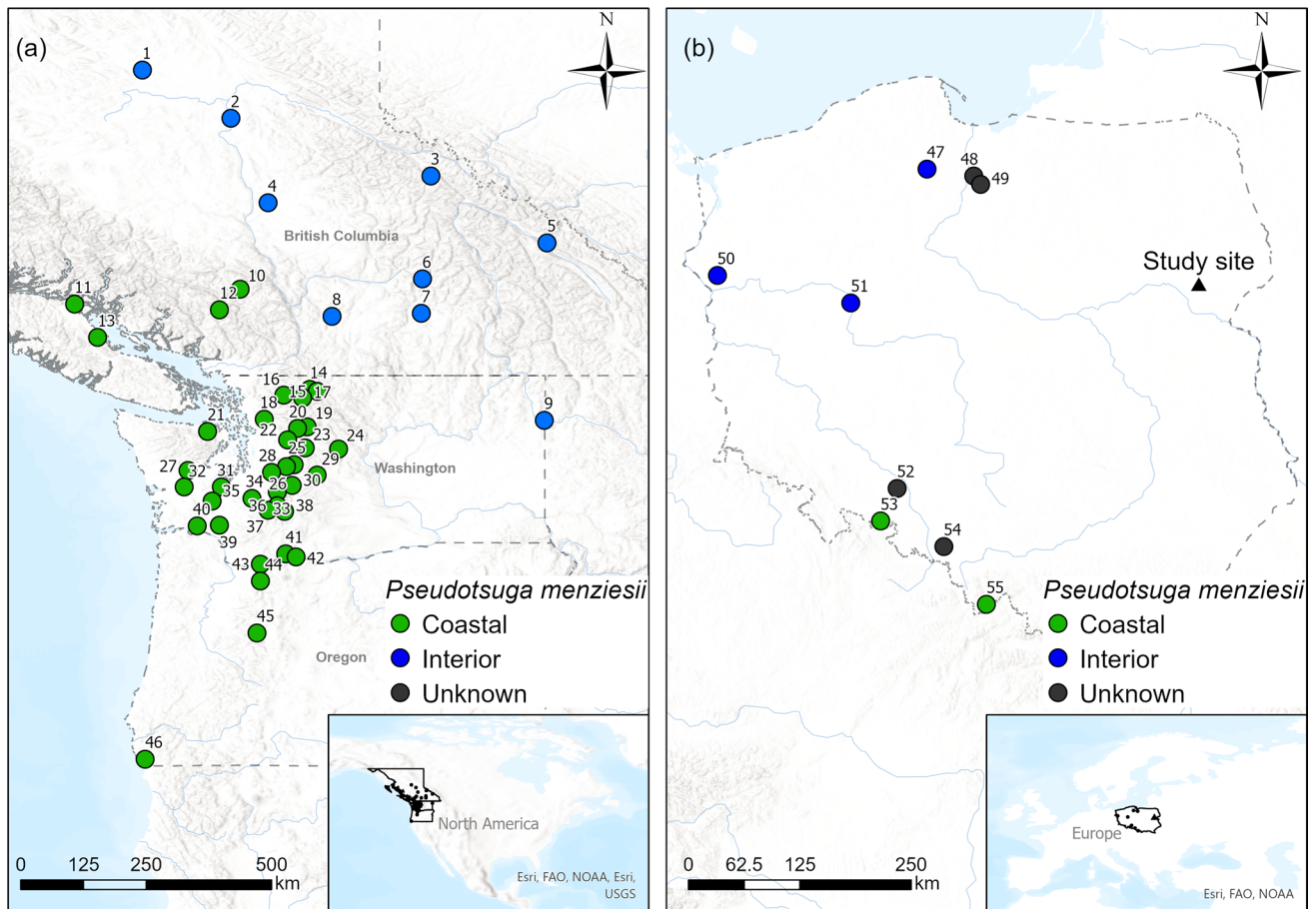
continental climate, representative for eastern Poland, i.e. the right-bank of Poland in the middle reaches of the Vistula River. This location was also the most continental (climatically severe) lowland test site established in Europe during the IUFRO Df campaign. The average long-term (1982–2012) temperature of the coldest month (January) was  $-5.0\text{ }^{\circ}\text{C}$  (extreme temperature recorded  $-35\text{ }^{\circ}\text{C}$ ), the average temperature of the warmest month (July) was  $17.3\text{ }^{\circ}\text{C}$ , and the average annual precipitation was 574 mm (Fig. 1).

The Rudka experimental test site was selected to estimate survival, frost resistance and productivity of Df provenances under suboptimal climatic conditions outside the Df planting zone in Europe. Frost hardiness was tested in 1978/79 during the juvenile development stage and was described in detail by Burzyński (1990).

Fifty-five seedlots of Df were included in the 1974 provenance trial with 38 seedlots originating from seeds collected during the 1966–67 IUFRO campaign – 12 provenances from the northern part of the species range in British Columbia (BC), Canada, 23 from Washington (WA) State and three from Oregon (OR) State, USA. In addition, eight operational seedlots were also collected in WA and included in the experiment (Fig. 2; Table 1). The Concrete provenance (WA) is represented by both seeds from the IUFRO collection (No. 16, Fig. 2), and from a commercial collection (No 14, Fig. 2). Overall, the experiment represents 35 seedlots from the coastal native range of Df and nine from the interior geographic range in western North America (Fig. 2).

**Fig. 1** Long-term (1982–2012) average monthly temperatures (+ maximal/-minimal, red bars) and average sum of precipitation for the studied region (Białystok meteorological station)





**Fig. 2** The locations of tested Douglas-fir provenances. The blue dots show the location of the interior Douglas-fir provenances; in latitudinal gradient (from north to south) provenances (**a** – North America); (**b** – Poland). The red dots show the location of the coastal Douglas-

fir provenances. The black dots (**b** in Poland) indicate landraces of unknown origin. The black triangle shows the location of the trial site (Rudka) in Poland

The progeny from nine previously established Df stands (now landraces), from unknown origins (Berney 1972; Hintsteiner et al. 2018) were also included in this provenance trial (Fig. 2). However, on the basis of cone and seed characteristics, it appears that stands located in Ujsoły and Pokrzywno correspond to coastal BC Df populations from the zone between 50° and 52°N (Berney 1972), while stands located in Biedrusko, Wirty and Dębno correspond to the interior Df variety (Burzyński 1990; Chylarecki 2004) (Fig. 2). We refer to those populations as landraces, although the concept of a landrace is broader and involves evolutionary adaptation of progeny to the new environment of introduction (Casañas et al. 2017). The introductions made to Poland have performed well, acclimating to the climatic conditions of their introduced location during > 80 years of growth (Burzyński 1990). Because conifer landrace populations may form quickly from the parent to offspring generation in new environments (Saxe et al. 2001), including seed from the landrace sources in our study provided a unique opportunity to

compare the performance of the progeny with the original provenances from the IUFRO collection and determine the suitability of these landraces as a future seed source.

The study layout was a completely randomized design (CRD) with 55 seedlots in 26–46 replications, depending on a varying number of seedlings available for planting.

Planting material was sown in the spring of 1970 and grown for four years at the Chojnów forest nursery, in Poland. A total of 1953 four-year-old seedlings were planted at the Rudka trial site at a 2 × 2 m spacing. The soil at the planting site was classified as a brown podsolic (Burzyński 1990). No thinnings were carried out over the 44 year trial.

## Measurements

Diameter at breast height (DBH; at 1.3 m) was measured on all living trees in 2005 (age 36 y); 2014 (45 y) and 2017 (age 48 y). In 2014 height (H) of all trees were measured while in



**Table 1** Geographical locations of tested Douglas-fir provenances. The column titled No. corresponds to the numbers of provenances provided on Fig. 2

No	Provenance Label*	Latitude [°N]	Longitude [°W]	Average elevation m a.s.l	MAT [°C]	MAP [mm]	No	Provenance Label	Latitude [°N]	Longitude [°W or °E for PL]	Average elevation m a.s.l	MAT [°C]	MAP [mm]
1	Fort. St. James [1-i-N-BC]	54°29'	124°15'	853	2.4	537	29	Cle Elum [29-c-N-WA]	47°13'	121°07'	640	7.5	1020
2	Stonner [2-i-N-BC]	53°37'	122°40'	579	4.7	636	30	Parkway [30-c-S-WA]	47°02'	121°34'	732	6.2	1877
3	Clemina [3-i-N-BC]	52°35'	119°05'	884	3.4	857	31	Tenino [31-c-S-WA]	47°00'	122°50'	21	10.4	1265
4	Williams Lake [4-i-N-BC]	52°06'	122°00'	610	5.6	413	32	Elma [32-c-S-WA]	47°00'	123°30'	75	10.6	1898
5	Golden [5-i-N-BC]	51°23'	117°00'	869	4.0	616	33	Voight Creek [33-c-S-WA]	46°55'	121°50'	515	2.6	2586
6	Salmon Arm [6-i-S-BC]	50°44'	119°14'	506	7.7	636	34	Alder Lake [34-c-S-WA]	46°48'	122°17'	427	9.4	1602
7	White Lake [7-i-S-BC]	50°07'	119°15'	518	3.0	794	35	Pe Ell [35-c-S-WA]	46°45'	123°00'	55	10.6	1290
8	Merritt [8-i-S-BC]	50°04'	120°51'	869	6.1	365	36	Randle [36-c-S-WA]	46°40'	121°50'	318	5.7	2163
9	Newport [9-i-N-WA]	48°12'	117°03'	732	7.7	688	37	Ashford [37-c-S-WA]	46°35'	122°00'	375	6.1	2394
10	D'Arcy [10-c-S-BC]	50°33'	122°30'	274	6.4	721	38	Packwood [38-c-S-WA]	46°34'	121°42'	305	8.9	1372
11	Stella Lake [11-c-S-BC]	50°17'	125°28'	152	8.2	1956	39	Castle Rock [39-c-S-WA]	46°19'	122°52'	152	10.3	1499
12	Alta [12-c-S-BC]	50°11'	122°52'	640	5.8	1211	40	Cathlamet [40-c-S-WA]	46°18'	123°16'	198	9.4	2094
13	Courtenay [13-c-S-BC]	49°41'	125°03'	67	9.3	1478	41	Willard [41-c-S-WA]	45°48'	121°41'	499	8.6	1436
14	Concrete [14-c-N-WA]	48°45'	121°15'	267	2.7	1529	42	Wind River [42-c-S-WA]	45°45'	121°30'	345	10.1	915
15	Diablo Dam [15-c-N-WA]	48°43'	121°07'	427	8.2	1561	43	Prindle [43-c-S-WA]	45°37'	122°08'	457	10.0	2137
16	Concrete [16-c-N-WA]	48°39'	121°43'	473	8.9	1831	44	Cherryville [44-c-N-OR]	45°19'	122°08'	671	9.0	2244
17	Bacon Point [17-c-N-WA]	48°36'	121°23'	503	9.0	1912	45	Upper Soda [45-c-N-OR]	44°23'	122°12'	991	8.9	1848
18	Arlington [18-c-N-WA]	48°13'	122°04'	91	10.2	1288	46	Brookings [46-c-S-OR]	42°07'	124°12'	305	12.8	2008
19	Sloan Creek [19-c-N-WA]	48°05'	121°18'	656	6.2	1927	47	Wirty [47-i-N-PL]	53°54'	18°10'	118	7.1	618
20	Perry Creek [20-c-N-WA]	48°03'	121°28'	610	6.7	2101	48	Ryjevo [48-u-N-PL]	53°50'	18°58'	30	7.8	615

Table 1 (continued)

No	Provenance Label*	Latitude [°N]	Longitude [°W]	Average elevation m a.s.l	MAT [°C]	MAP [mm]	No	Provenance Label	Latitude [°N]	Longitude [°W or °E for PL]	Average elevation m a.s.l	MAT [°C]	MAP [mm]
21	Louella [21-c-N-WA] Guard St	48°00'	123°05'	457	7.8	1446	49	Ośno	53°45'	19°05'	98	7.6	619
22	Gold Bar [22-c-N-WA]	47°51'	121°39'	122	10.3	1710	50	Dębno	52°45'	14°42'	50	8.9	503
23	Skykomish [23-c-N-WA]	47°42'	121°20'	305	6.8	2020	51	Biedrusko	52°32'	16°56'	90	8.6	505
24	Chiwaukum [24-c-N-WA]	47°41'	120°44'	549	7.6	781	52	Dąbrowa Opolska	50°40'	17°45'	160	8.4	608
25	Denny Creek [25-c-N-WA]	47°24'	121°32'	549	7.8	2001	53	Pokrzywno	50°20'	17°30'	630	8.0	613
26	Chester Morse Lake [26-c-N-WA]	47°22'	121°40'	606	8.1	2204	54	Paruszowiec	50°05'	18°30'	240	8.6	689
27	Matlock [27-c-N-WA]	47°18'	123°26'	499	9.1	2302	55	Ujsoły	49°30'	19°10'	650	5.9	1040
28	Enumclaw [28-c-N-WA]	47°16'	121°56'	244	9.8	1551							

\*The numerical labels sorted by latitude, starting with the northernmost locations; Douglas-fir variety: i-interior, c-coastal, u-unknown; the geographic and administrative location of the seed origin: N-northern, S-southern part of (a province/state/country) BC- British Columbia (Canada), WA- Washington (USA), OR- Oregon (USA), PL- Poland

2017 only 20% of trees were recorded (H) and 30 trees were randomly selected and harvested for the purpose of cross-sectional measurements. For harvested trees the diameters were taken with a caliper in the middle of 1 m-long sections from the bottom to the top of a tree to calculate individual tree volumes using the sectional method (V).

## Data analysis

For trees that were not measured for H in 2017, the height curve was fitted using the Näslund function (Näslund 1936):

$$H = \left( \frac{DBH}{\alpha + \beta * DBH} \right)^2 + 1.3, \quad (1)$$

where H represents tree height (m), DBH is the diameter at breast height (cm), and  $\alpha$ ,  $\beta$  are the fitted parameters.

We were concerned that standard volume equations available in the literature for *P. menziesii* might not be adequate enough for data obtained in this study; therefore, to develop a volume equation for the trees in our study, we used allometric functions commonly used in tree biomass and volume modelling (Sit and Poulin-Costello 1994) (we used Eq. 2 for measurements taken in 2014 (age 45 y) and 2017 (age 48 y), and Eq. 3 for measurements carried out in 2005 (age 36 y)):

$$\log_{10}(V) = \beta_0 + \beta_1 * \log_{10}(DBH) + \beta_2 \log_{10}(H) \quad (2)$$

$$\log_{10}(V) = \beta_0 + \beta_1 \cdot \log_{10}(DBH) \quad (3)$$

The parameters of these functions were fitted based on the individual tree volumes (V) obtained from the sectional measurement data. The parameters of Eqs. 2 and 3 and goodness of fit statistics for the allometric equations are listed in Table 2. The estimated parameters were then used in allometric functions to estimate the volume of all remaining individual trees for each provenance parameterized for a given age, using the measured DBH and H obtained from direct measurements (in 2014) or the height curve (in 2017). Stand productivity expressed as volume per hectare ( $V_{ha}$ ) was calculated using individual tree volumes for a given provenance taking its survival (S) into account. Mean annual increment of volume (MAI) was assessed as a  $V_{ha}$  for a given provenance divided by the final time point of our experiment, age 48.

To assess changes in the productivity of different provenances over time, which may be important in light of the recent accelerating climate change, we additionally estimated the periodic annual increment (PAI). Productivity of provenances was compared over two time intervals. The first interval was estimated based on  $V_{ha}$  at age 36 (time interval 1970–2005), and corresponded to PAI between 0 and 36 years. The second time interval estimated productivity

from 2005 to 2017, reflecting the current climate, and was calculated as the change in volume per ha of a given provenance between age 36 and 48, divided by the number of years designated as the growing period (12 years) (Avery and Burkhart 2015):

$$PAI = \frac{V_{ha2} - V_{ha1}}{T_2 - T_1} \quad (4)$$

where  $V_{ha}$  is the volume per area unit at times 1 and 2 and  $T_1$  represents the year starting the growth period, and  $T_2$  is the end year.

## Geographic and climatic data

Adaptation and the formation of local ecotypes/varieties through natural selection, gene flow, and other evolutionary processes are the outcome of long-term interactions between environmental conditions and local populations (Kawecki and Ebert 2004). Thus, to capture the environmental conditions under which Df provenances evolved, each provenance was characterized by geographic coordinates and bioclimatic factors. Geographic variables were used to represent constant, climate-determining factors (Molga 1986) that approximate genetic adaptation to local climate based on a longer time frame than modern climate data allows for. Geographic variables included latitude, elevation of seed origin, and longitude. Longitude, in our study, described the proximity to the ocean among seed sources from Df's native range in North America and was used to nuance differences between coastal and interior varieties (Table 1).

Bioclimatic variables which change more rapidly, especially during current climate change were in turn used to generate more biologically meaningful variables derived from monthly temperature and precipitation values (Läderach 2011). Climate conditions of the population origin were obtained from the WorldClim database (Fick and Hijmans 2017). Each population was characterized by the 19 bioclimatic variables representing long-term mean values. The dataset was obtained for the baseline period 1950–2000, which is available in the WorldClim database (Fick and Hijmans 2017). The bioclimatic variables represented annual trends (e.g., mean annual temperature, annual precipitation), seasonality (e.g., annual range in temperature and precipitation), and extreme or limiting environmental factors (e.g., temperature of the coldest and warmest month and precipitation of the wettest and driest quarter) (Läderach 2011; Fick and Hijmans 2017).

For clarity, we refer hereafter to each seed source tested in our study by the provenance name and provide the numerical labels sorted by latitude, starting with the northernmost locations. Each label also provides information on the

**Table 2** Fitted coefficients of two volume equations for Douglas-fir

Equation	R <sup>2*</sup>	MSE	RMSE	CV [%]	Parameter	Estimate	SE	−95%CI	+95%CI	p
2	0.997	0.001	0.038	0.121	b <sub>0</sub>	−4.306	0.126	−4.575	−4.036	<0.001
					b <sub>1</sub>	2.008	0.146	1.697	2.320	<0.001
					b <sub>2</sub>	0.872	0.230	0.381	1.363	0.002
3	0.989	0.002	0.052	0.286	b <sub>0</sub>	−3.896	0.089	−4.084	−3.708	<0.001
					b <sub>1</sub>	2.530	0.066	2.390	2.671	<0.001

\*R<sup>2</sup> coefficient of determination, MSE mean squared error of the estimate, RMSE root mean squared error, CV coefficient of variation, SE standard error, CI confidence intervals

geographic Df variety (interior (i)/coastal (c)/unknown (u)) and the geographic and administrative location of the seed origin, i.e., northern (N) or southern (S) part of a province/state/country (British Columbia (BC), Washington (WA), Oregon (OR), Poland (PL)). For example, the provenance White Lake is labelled as [7-i-S-BC] (number 7 on the map, Df interior type, southern British Columbia), which is consistent with the map numbers on Fig. 2 and data presented in Table 1. In general, labels numbered 1–9 refer to seed sources of Df interior type (i), while numbers 10–46 refer to the Df coastal variety (c) from the native range in North America. Numbers 47–55 refer to Polish landraces (Fig. 2, Table 1).

## Statistical analysis

Analysis of variance (ANOVA) was used to test for variation among examined provenances in mean DBH, H and V. The mathematical model for the single factor completely randomized design was applied, according to the following equation:

$$x_{ij} = \mu + \alpha_i + \varepsilon_{ij} \quad (5)$$

where  $x_{ij}$  is a dependent variable,  $\mu$  represents mean value of the dependent variable,  $\alpha_i$  is an effect of provenance,  $\varepsilon_{ij}$  represents random error.

When the ANOVA indicated a significant provenance effect, the Tukey's HSD test was used ( $\alpha=0.05$ ) to test for differences in mean values among provenances.

To compare the rank order of provenances in PAI between the two time intervals considered, i.e. PAI between 1970–2005 and PAI between 2005–2017, we computed the nonparametric statistics: the Kendall rank correlation coefficient and Spearman's Rank Correlation Coefficient. Before conducting the analysis, the PAI data expressed in a quantitative scale was scaled up to ordinal data.

To further explore the dataset and classify the provenances according to their similarity/distance, cluster analysis was used based on the standardized data obtained for

individual tree V and S. The Euclidean distance was used as a distance metric, and the Unweighted Pair Grouping Method with Arithmetic-mean (UPGMA) was chosen as a clustering criterion. The UPGMA is one of the most commonly used variants of the Globally Closest Pair clustering algorithm, defining the dissimilarity between clusters as their average dissimilarity (Gronau and Moran 2007).

The relationships between DBH, H,  $V_{ha}$  and S and the predictor geographic and climatic variables were modelled using the generalized additive models (GAM, Eq. 6) (Hastie and Tibshirani 1990), which is a non-parametric extension of the generalized linear models (GLM). We chose this statistical approach because it enables exploration of the shapes of response curves for Df provenances to environmental gradients and allows fitting of statistical models that are in better agreement with ecological theory (Frescino et al. 2001; Austin 2002; Lehmann et al. 2002; Guisan et al. 2006; Aertsens et al. 2010). GAM uses transformation procedures that are independent for each predictor variable, which are summed to calculate the response variable according to the equation (Guisan and Zimmermann 2000):

$$G(E(Y)) = \beta + f_1(X_1) + f_2(X_2) + f_3(X_3) + f_n(X_n) \quad (6)$$

where Y is the dependent variable, ( $X_i$ ) are the predictor variables, (G) is the link function,  $f_1, f_2, \dots, f_n$  are smoothing spline functions estimated from the data,  $\beta$  is the free term. An identity link function was specified for the normally distributed response data. Predictor variables entered the models individually using a smoothing spline with four degrees of freedom. The optimal amount of smoothing was estimated based on cross-validation. The geographic and climatic trends were modelled separately. The predictor variables in the geographic models were latitude, longitude and elevation of the provenance origin in the natural range of Df. The local landraces were excluded from the model for geographic data. All 19 bioclimatic characteristics were taken into account in the climatic models. To determine the importance of bioclimatic variables and establish the final set of predictors for modeling, we applied the method to determine the importance of variables using the R language



package VIP (R Core Team, 2020). VIP is a general framework for constructing variable importance plots from various types of models in R.

Aside from some standard model-specific variable importance measures, VIP also provides model agnostic approaches, which include: 1) an efficient permutation-based variable importance measure, 2) variable importance based on Shapley values (Štrumbelj and Kononenko 2014), and 3) the variance-based approach (Greenwell et al. 2018). The selection of the best model, i.e. the model containing independent variables which explained the largest amount of observed variance, was based on the adjusted coefficient of determination/model efficiency ( $R^2_{adj}$ ). Graphs of smoothing spline functions of GAM models were used to illustrate the effect of individual predictor variables on dependent variables. Homoscedasticity of the model was analysed using a scatterplot of the standardized residuals against each of the independent variables. The statistical analyses were performed using the statistical package Statistica 13 (StatSoft Inc.).

## Results

### Survival rate

The survival rate at the Rudka trial site was highly variable between Df provenances (Fig. 3, Table 3). At age 36, the average survival was 42% with the highest survival observed for the provenances from Newport [9-i-N-WA] (91%), Cle Elum [29-c-N-WA] (89%), White Lake [7-i-S-BC] (89%), Golden [5-i-N-BC] (86%) and Wirty [47-i-N-PL] (86%). All provenances with the highest survival except for Cle Elum represented the interior variety of Df. On the other hand, the coastal provenances from more southern locations: Pe Ell [35-c-S-WA] and Cathlamet [40-c-S-WA], Brookings [46-c-S-OR], as well as Ujsoty [55-c-S-PL] and Dąbrowa Opolska [52-u-S-PL], had a survival rate below 10%. At age 48 the overall survival rate at the study site dropped to 22%, with 13 provenances experiencing 100% mortality. At the last assessment the highest survival rate was recorded for the provenances from Wirty [47-i-N-PL] (75%), White Lake [7-i-S-BC] (71%) and Salmon Arm [6-i-S-BC] (69%, Fig. 3, Table 3), all representing the interior variety of Df.

### Productivity-related characteristics

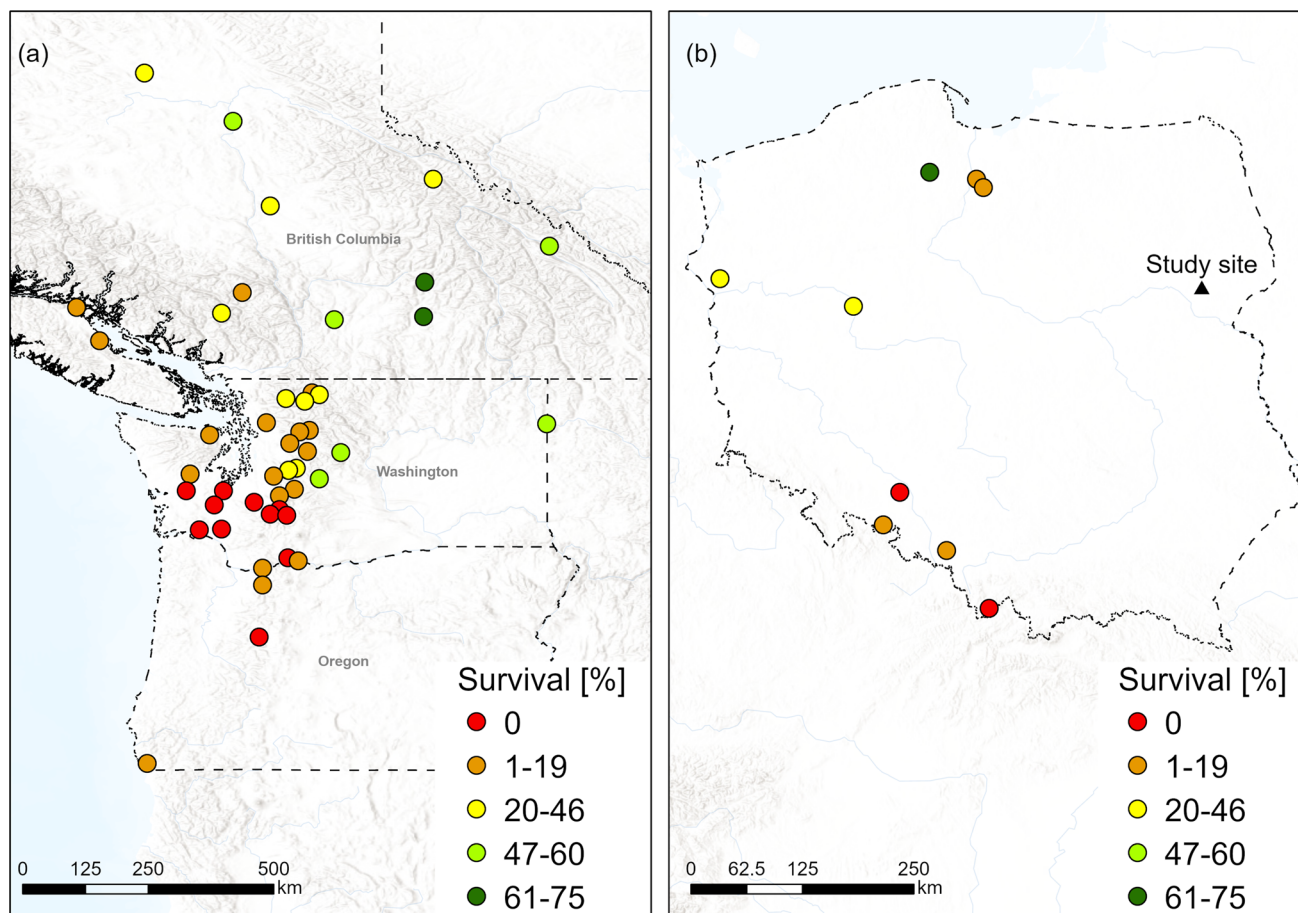
All biometric traits we measured at the Rudka site varied significantly within the provenances examined (Table 3). The mean DBH at age 36 years ranged from 4.6 cm for Packwood [38-c-S-WA], to 24 cm for Biedrusko [51-i-N-PL], a local landrace. At age 36 the Biedrusko landrace also had the

largest individual tree stem volume, which was significantly greater than for all other provenances.

At age 48, the Biedrusko landrace maintained its dominant position for DBH, H and individual stem V. The other provenances with stem volumes above the average were: White Lake [7-i-S-BC] and Salmon Arm [6-i-S-BC] from the continental, interior part of BC, Bacon Point [17-c-N-WA], Skykomish [23-c-N-WA] and Matlock [27-c-N-WA] from WA, and Wirty [47-i-N-PL] in Poland (Table 3).

Taking into account the survival, the mean stand volume at age 36 was  $120 \text{ m}^3 \text{ ha}^{-1}$ . The largest volume was recorded for the White Lake [7-i-S-BC] ( $623 \text{ m}^3 \text{ ha}^{-1}$ ), Wirty [47-i-N-PL] ( $564 \text{ m}^3 \text{ ha}^{-1}$ ) and Salmon Arm [6-i-S-BC] ( $545 \text{ m}^3 \text{ ha}^{-1}$ ) provenances (Fig. 4). These three provenances maintained their high productivity, and by age 48 stand volume reached 1216; 952; and  $1112 \text{ m}^3 \text{ ha}^{-1}$  respectively (White Lake, Wirty, Salmon Arm), while the average volume for all provenances combined did not exceed  $280 \text{ m}^3 \text{ ha}^{-1}$ . Figure 5 illustrates the geographic pattern of variation among the studied populations for stand volume. It is clear that seed sources from coastal BC, WA, and west of the Cascades showed the poorest performance. The only two provenances from those regions with a  $V_{ha}$  above the average were Bacon Point [17-c-N-WA] and Chester Morse Lake [26-c-N-WA] (Figs. 4 and 5). All other populations with an above-average  $V_{ha}$  at age 48 were from interior BC and WA or east of the Cascades, and the Polish landraces originating from the interior variety (Figs. 4 and 5).

The volume per unit area measurements provided MAI values calculated at the final time point of our experiment, age 48. The average  $MAI_{48}$  was  $4.41 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ , while the best performing provenances, White Lake [7-i-S-BC] and Salmon Arm [6-i-S-BC], attained an  $MAI_{48}$  of 25.34 and  $23.16 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ , respectively (Fig. 4). The changes in annual volume increment were also considerable between the two time intervals considered. The first time interval covered the younger stages of tree growth, at age 0–36 years, while the second time interval referred to the high pole stand stage, within the range of 36–48 years. The average  $PAI_{0-36}$  for the provenances tested was  $3.33 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ , while the average  $PAI_{36-48}$  reached  $7.65 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$  and coincided with the period of intensive volume increment. The  $PAI_{36-48}$  for the provenances with the greatest productivity, White Lake and Salmon Arm, reached exceptional growth rates of 49.34 and  $47.02 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ , respectively, indicating a continuous increase in their annual volume increment and successful competition with neighbouring trees, reinforcing their dominant positions in the stand (Fig. 4). In general, the Spearman's rank correlation coefficient ( $0.853, p < 0.001$ ), and the Kendall's tau coefficient ( $0.648, p < 0.001$ ) indicated a significant association between rank orders in PAI for the two time intervals considered. However, it is important to note that some provenances such as Bacon Point



**Fig. 3** Diversity of the survival rate in the tested populations from **a** the US and Canada and **b** the local landrace populations in Poland

[17-c-N-WA], Chester Morse Lake [26-c-N-WA] and Chiwaukum [24-c-N-WA] changed their rank order due to an increase in productivity during the second time interval (an increase of 9, 11 and 7 positions, respectively, in the  $PAI_{36-48}$  ranking compared to the ranking for  $PAI_{0-36}$ ) relative to other provenances (Table 3).

A cluster analysis based on the volume of individual trees and survival rate at age 48 revealed five distinct performance classes (Fig. 6). Trees in cluster 1, consisted of the best performing provenances, White Lake [7-i-S-BC], Salmon Arm [6-i-S-BC] and Wirty [47-i-N-PL], which were characterized by both the highest volume and survival rate, while trees in cluster 2 exhibited above average volume and survival. Cluster 3 gathered the worst performing provenances that did not survive to age 48. Provenances in cluster 4 had low survival (5.5–18.4%) and average volume, while provenances in cluster 5 had below average survival (24.3–45.5%) and above average productivity (Fig. 6). The geographical distribution of the populations belonging to individual clusters are shown in Fig. 7.

### Geographical trends

All geographic characteristics, i.e. latitude, longitude and elevation of seed sources, significantly impacted the growth and survival rate of provenances at the Rudka study site. The highest portion of variation (Table 4) was explained by survival rate (> 80%) and stand volume (> 77%). As the  $V_{ha}$  was calculated on the basis of both productivity-related traits (DBH and H) and survival rate, we further present the results of the GAM analysis for  $V_{ha}$  at age 48 years only.

The partial effects of the geographic variables on stand volume were estimated from the spline functions presented in Fig. 8. The fitted smooth function showed a significant effect when confidence intervals (CI) did not include zero. More northern origin seed sources positively affected stand volume, and the largest positive effect on the dependent variable, i.e. an increase of approximately  $59 \text{ m}^3 \text{ ha}^{-1}$  per  $1^\circ$  of latitude, was observed in the latitude range between  $47\text{--}54^\circ\text{N}$  (Fig. 8a). In general, provenances from the range of  $50\text{--}54^\circ\text{N}$  had significantly higher stand volumes than seed sources from the range of  $42\text{--}48^\circ\text{N}$ . In terms of the effect of longitude on stand productivity, the best performing

**Table 3** Per cent survival (S, %), diameter (DBH, cm), height (H, m) and volume per individual tree (V, m<sup>3</sup>) and periodic annual increment (PAI) ranking of provenances at age 36, 45, and 48 years at the Rudka test site. The same letters indicate statistically homogenous groups (Tukey's HSD test,  $\alpha=0.05$ )

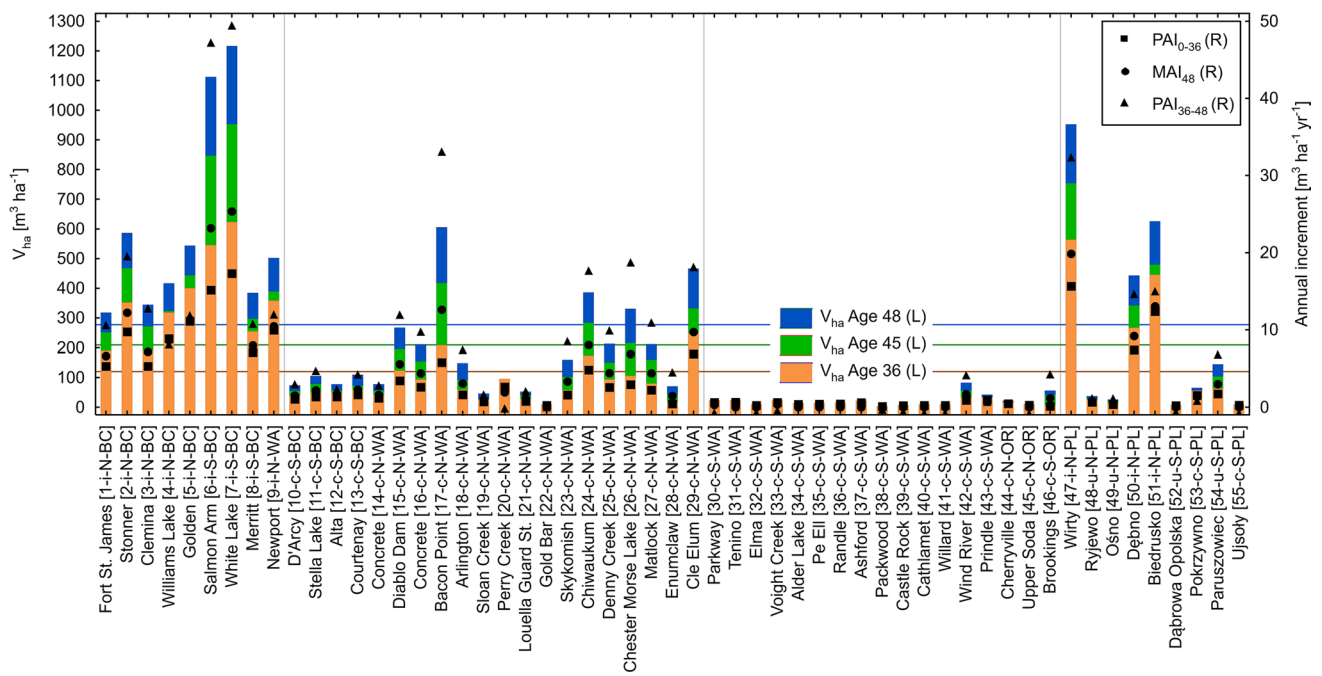
Provenance*	Label*	Age 36 y					Age 45 y					Age 48 y				
		S [%]	DBH [cm]	V [m <sup>3</sup> ]	PAI <sub>0-36</sub> rank	H [m]	S [%]	DBH [cm]	V [m <sup>3</sup> ]	H [m]	S [%]	DBH [cm]	V [m <sup>3</sup> ]	H [m]	V [m <sup>3</sup> ]	PAI <sub>36-48</sub> rank
Fort St. James	[1-i-N-BC]	64	13.6 abcde	0.12 abcd	14	18.6 ab	15 abcd	0.221 ab	45	19.3 ab	17.3 abc	0.279 ab	17			
Stonner	[2-i-N-BC]	75	16.1 cdef	0.187 abcd	7	22.6 abc	16.9 abcd	0.336 ab	56	23.6 abc	19.5 abc	0.422 ab	5			
Clemina	[3-i-N-BC]	68	12.1 abcde	0.113 abcd	13	21.2 abc	16.3 abcd	0.305 ab	35	22.2 abc	18.7 abc	0.388 ab	11			
Williams Lake	[4-i-N-BC]	70	16.1 cdef	0.183 abcd	8	20.8 abc	15.1 abcd	0.284 ab	45	21.6 abc	18.4 abc	0.366 ab	21			
Golden	[5-i-N-BC]	86	15.9 bcdef	0.186 abcd	5	21.8 abc	16.2 abcd	0.304 ab	58	22.3 abc	18.9 abc	0.372 ab	14			
Salmon Arm	[6-i-S-BC]	79	18.8 ef	0.275 cd	3	26.3 bc	18.1 bc	0.49 abc	69	28 bc	20.9 bc	0.643 abc	2			
White Lake	[7-i-S-BC]	89	18.3 def	0.281 de	1	26.2 bc	18.3 c	0.534 bc	71	28.1 bc	20.7 bc	0.681 bc	1			
Merritt	[8-i-S-BC]	81	14.2 abcde	0.126 abc	10	18.8 ab	14.5 ad	0.204 a	58	19.4 ab	17.6 abc	0.263 a	16			
Newport	[9-i-N-WA]	91	14.8 abcdef	0.158 abcd	6	20.5 ab	15.2 abcd	0.262 ab	59	21.2 abc	18.3 abc	0.338 ab	12			
D'Arcy	[10-c-S-BC]	31	9.4 abcde	0.049 abcd	30	16.4 abc	13.3 abcd	0.159 ab	14	17.2 abc	16.1 abc	0.211 ab	29			
Stella Lake	[11-c-S-BC]	39	8.5 abc	0.049 abc	28	17.6 abc	16.3 abcd	0.205 abc	15	19.5 abc	17.5 abc	0.277 abc	24			
Alta	[12-c-S-BC]	57	8.5 ab	0.034 a	27	12.9 a	13 ab	0.093 ab	24	14 a	14.3 a	0.127 ab	31			
Courtenay	[13-c-S-BC]	42	8.8 abc	0.056 ab	24	15.7 ab	14.6 abcd	0.173 ab	17	18.5 abc	16.8 abc	0.261 ab	27			
Concrete	[14-c-N-WA]	42	11.5 abcde	0.09 abcd	29	17.8 ab	15.6 abcd	0.222 ab	28	19.6 ab	17.2 abc	0.303 ab	30			
Diablo Dam	[15-c-N-WA]	67	10.4 abc	0.074 a	16	17.8 ab	15 abcd	0.216 ab	36	19.5 ab	17.3 abc	0.296 ab	13			
Concrete	[16-c-N-WA]	37	9.3 abcd	0.047 ab	19	15 ab	12.6 abc	0.121 ab	18	15.8 ab	15.5 ab	0.166 ab	19			
Bacon Point	[17-c-N-WA]	63	13.2 abcde	0.133 abcd	12	23.3 abc	17.7 abcd	0.418 abc	40	26.5 abc	20.1 abc	0.605 abc	3			
Arlington	[18-c-N-WA]	43	8.9 abc	0.055 ab	23	18 abc	14.5 abcd	0.213 ab	17	20.5 abc	17.6 abc	0.344 abc	22			
Sloan Creek	[19-c-N-WA]	47	6.7 a	0.022 a	34	14.2 ab	12 abcd	0.096 ab	11	16.4 abc	16.1 abc	0.164 abc	33			
Perry Creek	[20-c-N-WA]	54	9.4 abc	0.07 a	18	18.3 abc	16.2 abcd	0.21 abc	14	20 abc	18 abc	0.274 abc	40			
Louella Guard St	[21-c-N-WA]	31	7.2 abc	0.036 abcd	33	22.1 abc	16 abcd	0.286 abc	6	23.3 abc	19.7 abc	0.375 abc	32			
Gold Bar	[22-c-N-WA]	17	7.1 abcde	0.021 abcd	50	10.7 abc	14 abcd	0.058 abc	6	11.5 abc	12.8 abc	0.062 abc	39			
Skykomish	[23-c-N-WA]	27	10.1 abcde	0.084 abcd	25	25.5 abc	18.3 abcd	0.448 abc	9	29.3 abc	21.5 abc	0.702 abc	20			
Chiwaukum	[24-c-N-WA]	69	11.8 abcde	0.101 abc	15	18.4 ab	14.9 abcd	0.213 ab	53	19.7 ab	17.6 abc	0.29 ab	8			
Denny Creek	[25-c-N-WA]	50	10.2 abcd	0.075 abc	20	17.2 ab	14.8 abcd	0.204 ab	29	19.1 ab	16.9 abc	0.289 ab	18			
Chester Morse Lake	[26-c-N-WA]	53	10.6 abcd	0.08 ab	17	20 ab	16.1 abcd	0.282 ab	31	22.8 abc	18.7 abc	0.432 abc	6			
Matlock	[27-c-N-WA]	34	10.2 abcde	0.093 abcd	21	22.7 abc	18.1 abcd	0.446 abc	14	25.7 abc	19.6 abc	0.591 abc	15			
Enumclaw	[28-c-N-WA]	23	7.7 abcde	0.027 abcd	42	21.5 abc	16.6 abcd	0.295 abc	6	24.8 abc	19.8 abc	0.488 abc	25			
Cle Elum	[29-c-N-WA]	89	12.9 abcde	0.112 ab	11	19 ab	15.4 abcd	0.232 a	57	20.7 ab	18 abc	0.326 ab	7			
Parkway	[30-c-S-WA]	40	6.9 ab	0.023 a	37	13 abc	12.9 abcd	0.079 abc	6	13.8 abc	14.6 abc	0.1 abc	45			
Tenino	[31-c-S-WA]	26	7.3 abcd	0.037 abcd	35				0				55			
Elma	[32-c-S-WA]	19	6.5 abcde	0.019 abcd	51				0				46			
Voight Creek	[33-c-S-WA]	24	8.3 abcde	0.039 abcd	38	12 abc	12.1 abcd	0.067 abc	6	14.7 abc	15.1 abc	0.12 abc	42			
Alder Lake	[34-c-S-WA]	17	7.8 abcde	0.032 abcd	44				0				51			
Pe Ell	[35-c-S-WA]	8	8.8 abcdef	0.072 abcde	43				0				52			

Table 3 (continued)

Provenance*	Label*	Age 36 y				Age 45 y				Age 48 y				PAI <sub>36-48</sub> rank
		S [%]	DBH [cm]	V [m <sup>3</sup> ]	PAI <sub>0-36</sub> rank	DBH [cm]	H [m]	V [m <sup>3</sup> ]	S [%]	DBH [cm]	H [m]	V [m <sup>3</sup> ]	PAI <sub>36-48</sub> rank	
Randle	[36-c-S-WA]	22	7.9 abcde	0.028 abcd	41				0				53	
Ashford	[37-c-S-WA]	15	9.9 abcdef	0.059 abcd	39				0				54	
Packwood	[38-c-S-WA]	26	4.6 abc	0.006 abcd	55				0				41	
Castle Rock	[39-c-S-WA]	16	5.9 abcde	0.019 abcd	53				0				43	
Cathlamet	[40-c-S-WA]	3	15.9 abcdef	0.139 abcde	49				0				47	
Willard	[41-c-S-WA]	20	7 abcde	0.018 abcd	48				0				48	
Wind River	[42-c-S-WA]	24	8.9 abcde	0.055 abcd	32	15.1 ab	13.7 abcd	0.151 ab	15	16.9 abc	15.8 abc	0.223 ab	28	
Prindle	[43-c-S-WA]	34	8.3 abc	0.039 abc	31	14.9 abc	12.3 abcd	0.109 ab	11	15.6 abc	15.6 abc	0.146 abc	37	
Cherryville	[44-c-N-OR]	31	7.1 abc	0.022 ab	40	12.9 abc	11.9 abcd	0.077 abc	6	15.8 abc	15.7 abc	0.154 abc	38	
Upper Soda	[45-c-N-OR]	24	6.4 abc	0.017 abcd	46				0				50	
Brookings	[46-c-S-OR]	8	10.4 abcdef	0.048 abcde	54	18.8 abc	14.7 abcd	0.21 abc	4	20.2 abc	18 abc	0.29 abc	26	
Wirty	[47-i-N-PL]	86	18.8 ef	0.262 bcd	2	23.9 abc	17.5 abcd	0.402 abc	75	25.1 abc	19.9 abc	0.508 abc	4	
Ryjewo	[48-u-N-PL]	24	7.9 abcde	0.04 abcd	36	18.1 abc	16.5 abcd	0.193 abc	6	19.9 abc	18.2 abc	0.253 abc	34	
Ośno	[49-u-N-PL]	16	7.9 abcde	0.031 abcd	45	15.3 abc	14.9 abcd	0.126 abc	6	16.8 abc	16.5 abc	0.166 abc	35	
Dębno	[50-i-N-PL]	59	15.2 bcdef	0.182 abcd	9	20.8 abc	16 abcd	0.315 ab	43	22 abc	18.3 abc	0.407 ab	10	
Biedrusko	[51-i-N-PL]	35	23.9 f	0.507 e	4	33 c	19.1 d	0.789 c	24	34.8 c	23 c	1.028 c	9	
Dąbrowa Opolska	[52-u-S-PL]	6	9.9 abcdef	0.056 abcde	52				0				44	
Pokrzywno	[53-c-S-PL]	48	8.2 abc	0.046 a	26	17.2 abc	14.5 abcd	0.204 abc	10	18.2 abc	16 abc	0.27 abc	36	
Paruszowiec	[54-u-S-PL]	24	11.3 abcde	0.103 abcd	22	20.4 abc	15.7 abcd	0.341 abc	12	22.2 abc	17.9 abc	0.476 abc	23	
Ujsoty	[55-c-S-PL]	6	9 abcdef	0.064 abcde	47				0				49	
Mean		42.1	12.2	0.1		20.9	16.0	0.3	22.2	22.4	18.6	0.4		
SD		0.2	7.1	0.2		7.6	3.2	0.3	0.4	8.3	3.6	0.4		
CV [%]		139.1	58.4	139.1		36.3	20.0	87.1	86.8	37.2	19.6	86.8		

Label\* the numerical labels sorted by latitude, starting with the northernmost locations; Douglas-fir variety: i-interior, c-coastal, u-unknown; the geographic and administrative location of the seed origin: N-northern, S-southern part of (a province/state/country) BC-British Columbia (Canada), WA-Washington (USA), OR-Oregon (USA), PL-Poland





**Fig. 4** Stand volume on an area basis for individual Douglas-fir provenances at the Rudka test site, taking into account the survival rate. Provenances without symbols beyond age 36 were no longer repre-

sented at the trial. Horizontal lines denote the average stand volume at a particular age

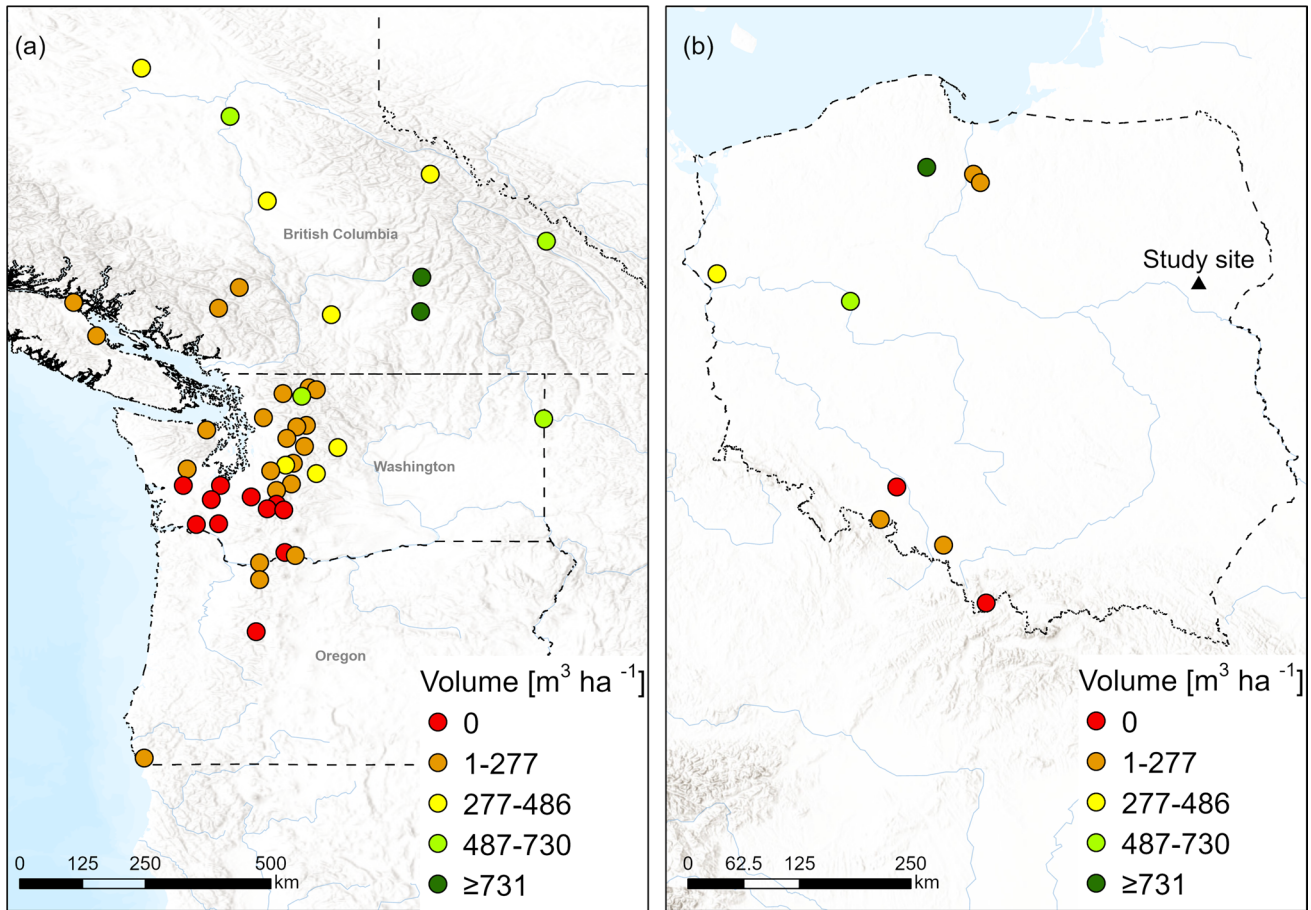
provenances were from continental origins (117–120°W). The western locations, from the Pacific Coast Range, negatively affected stand volumes at Rudka (Fig. 8b). The sharpest decreasing trend for the dependent variable was found for longitudes between 119–121°W. In this range, the estimated stand volume decreased by 213 m<sup>3</sup> ha<sup>-1</sup> per 1° of longitude, along the gradient from the continental/interior longitudes (with the highest volumes) to the Pacific Coast locations (121–126°W). The elevation of seed sources positively affected stand volume for the origins up to ~700 m a.s.l., with the optimum at around 500 (400–650) m a.s.l.. Further increases in altitude in the range of 675–900 m a.s.l. resulted in a slight negative trend in which estimated volume decreased by 190 m<sup>3</sup> ha<sup>-1</sup> (Fig. 8c).

**Climatic trends**

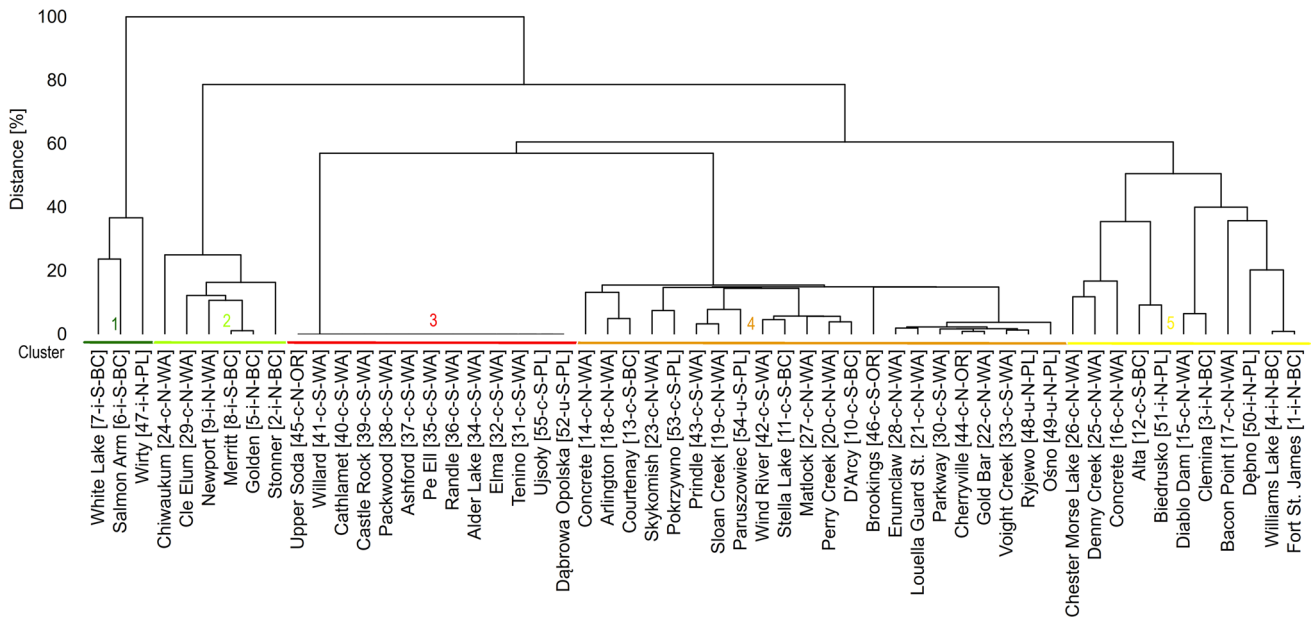
We found that the greatest variation in productivity-related traits was explained using five bioclimatic variables: annual mean temperature (MAT), temperature annual range (continentality), mean annual precipitation sum (MAP), isothermality, which quantifies the day-to-night temperature oscillations relative to the summer-to-winter (annual) oscillations, and precipitation seasonality (PS coef. of variance). These variables jointly explained, in various years of measurement, from 54.6 to 62.2% of the variance in DBH, approximately 57% of the variance in H, and 65% of the variance in V<sub>ha</sub>, and from 65.9 to 70.7% in survival (Table 5). As the V<sub>ha</sub> was

calculated on the basis of both productivity-related traits (DBH and H) and survival, we further present the results of the GAM analysis for the V<sub>ha</sub> at age 48 years only (Fig. 9).

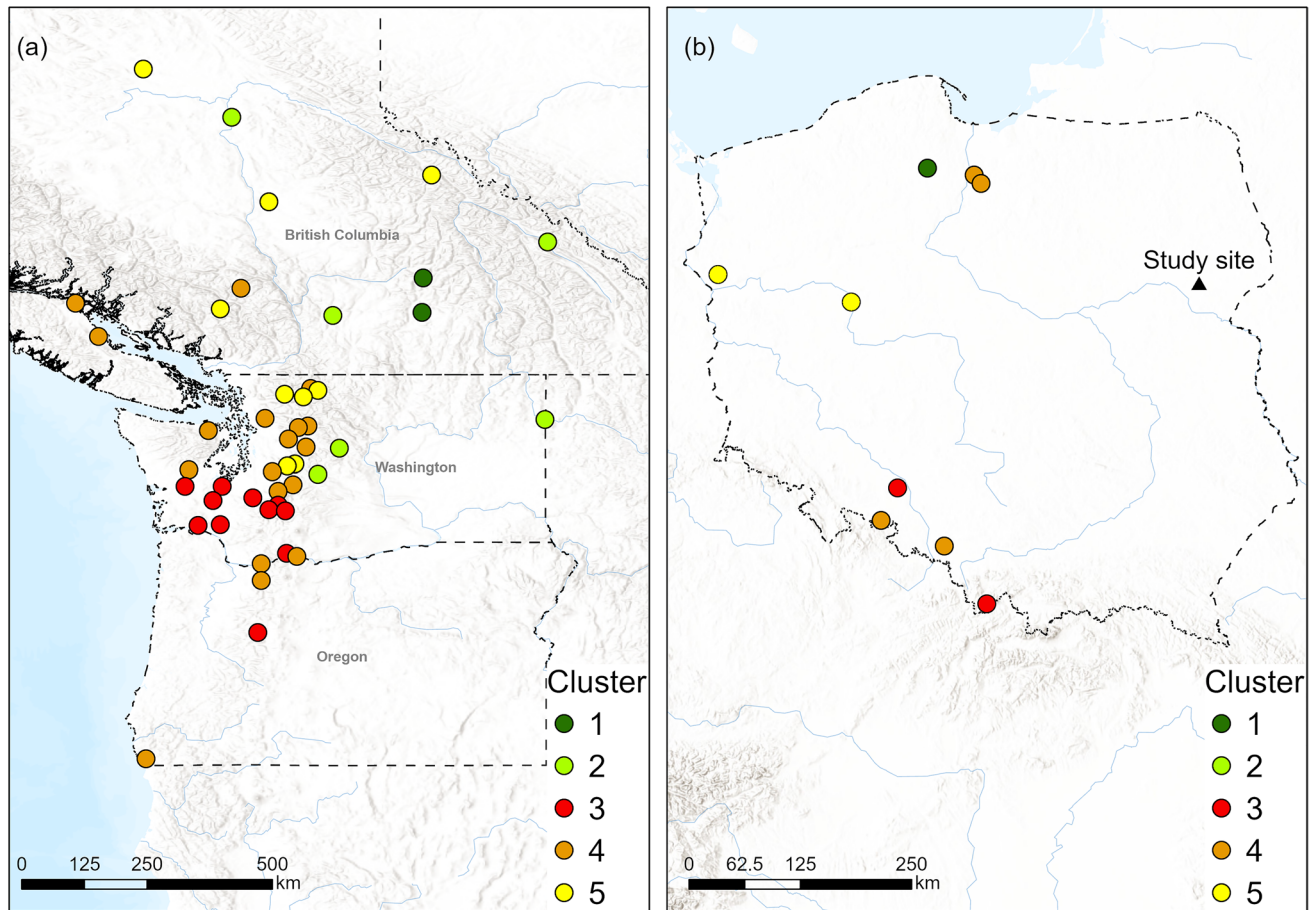
The partial effects of the investigated climatic variables on productivity at age 48 expressed by V<sub>ha</sub> are presented in Fig. 9. The largest partial effect among selected climatic variables was observed for precipitation seasonality. The increase in the index of the precipitation seasonality from 25 to 45 resulted in a rapid decrease in productivity (Fig. 9d). However, from the value of the index of 50, a further increase in precipitation seasonality did not result in changes in productivity. The partial effect of this variable on productivity was positively associated with seed sources originating from sites with less variation in precipitation during the year than at Rudka. The partial effect of the mean annual precipitation (MAP) was relatively weak in the entire range of precipitation values, however, increasing values of this variable showed a positive effect on productivity (Fig. 9c). Similarly, a positive effect was observed in the case of the continentality index and mean annual temperature (MAT) variables. In both cases, the confidence intervals included a zero value over the entire range of X-axis values, although the increase in continentality index of the population origin from 22 to 36 resulted in an increase in productivity of approximately 300 m<sup>3</sup> (Fig. 9a). A similar increase in productivity was observed when MAT of the origin increased from 5 to 9 °C with no further positive effect for higher MAT values (Fig. 9b).



**Fig. 5** Diversity in stand volume ( $m^3/ha$ ) at age 48 in the tested populations from **a** the United States and Canada and **b** Poland



**Fig. 6** Clustering of 55 provenances of Douglas-fir based on volume of individual trees and survival rate at age 48 at the test site in Rudka, Poland



**Fig. 7** Spatial distribution of provenances grouped in clusters based on volume of individual trees and survival rate at age 48

**Table 4** The results of the GAM analysis (adjusted coefficient of determination  $R^2_{adj}$ ) based on all geographical characteristics for diameter at breast height (DBH, cm), height (H, m), volume per hectare ( $V_{ha}$ ,  $m^3 ha^{-1}$ ) and survival (S, %)

Age [years]	DBH [cm]	H [m]	$V_{ha}$ [ $m^3 ha^{-1}$ ]	S [%]
36	64.3	–	81.1	86.3
45	64.7	62.7	78.3	80.3
48	61.4	62.0	77.4	80.3

The effect of isothermality showed a variable effect on productivity. The highest productivity was associated with the isothermality index from approximately 30–37% (Fig. 9e). The decrease or increase in isothermality beyond this range resulted in a decrease in productivity.

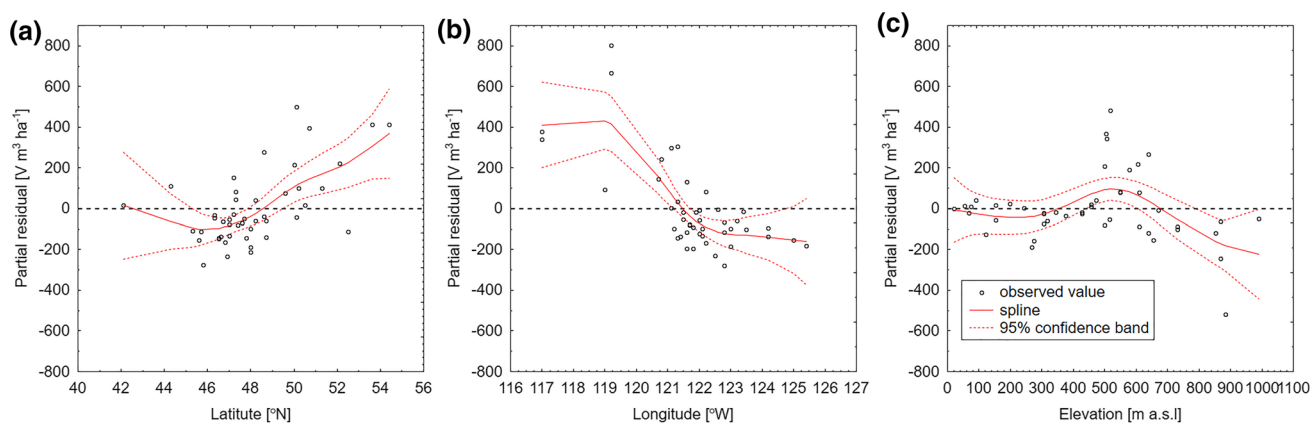
### Discussion

Our study showed considerable variation in survival and productivity-related traits among examined Df seed sources in the continental climatic conditions of eastern Poland.

These results emphasize the importance of selecting appropriate provenances for use at particular locations to ensure the optimum survival, productivity and resilience of planted forests in the long-term. The analysis relating geographic location and climatic variables at the area of origin of Df populations with the responses in growth parameters at the Rudka test site in eastern Poland sheds light on the capacity for within-species adaptation and can facilitate the interpretation of results for species introductions and limitations of seed source selections.

Df provenances from interior BC, WA and the progeny of the landrace stand in Wirty [47-i-N-PL], showed the best performance to conditions at the Rudka study site located in the continental climate of eastern Poland. In contrast, most provenances from the coastal Df range exhibited maladaptation to climatic conditions at the test site, which was reflected by the high mortality of trees and/or their low productivity. Our findings are in clear contrast to most European studies, where Df populations originating from coastal BC, the west side of the Cascade Range and coastal regions of WA and OR are recommended for Europe (Kleinschmit and Bastien 1992; Isaac-Renton et al. 2014; Chakraborty





**Fig. 8** Spline-curves showing the partial effects of **a** latitude, **b** longitude, and **c** elevation on a volume per ha basis in Douglas-fir at age 48 years ( $R^2=77.4\%$ ) at the Rudka test site

**Table 5** Adjusted coefficients of determination ( $R^2_{adj}$ ) in the GAM analysis based on five bioclimatic variables: annual mean temperature (MAT), isothermality, temperature annual range (continentality), mean annual precipitation (MAP) and precipitation seasonality (PS coef. of variance) explaining jointly the largest amount of variation (among 19 bioclimatic variables tested) in diameter at breast height (DBH, cm), height (H, m), volume per hectare ( $V_{ha}$ ,  $m^3 ha^{-1}$ ) and survival (S, %) for three ages at the Rudka test site

Age [years]	DBH [cm]	H [m]	$V_{ha}$ [ $m^3 ha^{-1}$ ]	S [%]
36	62.2	—	66.2	65.9
45	56.6	57.7	65.2	70.7
48	54.6	56.9	64.2	70.7

et al. 2015, 2016). In these studies, projecting the potential provenance performance (expressed as either dominant height or basal area), in relation to climate at the origin and planting sites, some interior Df sources were also identified as optimal, but with limited supporting evidence for such recommendations (Chakraborty et al. 2016). Moreover, the set of independent data on which the model was evaluated lacked the low-elevation sites with a continental climate (Chakraborty et al. 2016), making our observations particularly important in the context of selection decisions and recommendations regarding optimal Df sources for lowland sites with continental climates.

A group of 10 populations originating from south-eastern WA, one from OR, and two landrace populations (Dąbrowa Opolska [52-u-S-PL] and Ujsoły [55-c-S-PL]) had 100% mortality by age 48 at the test site. The research carried out in winter 1978/79 at Rudka indicated that frost susceptibility was the major contributor to sapling mortality at the early stage of this experiment (Burzyński 1990). These observations correspond well with the geographical patterns of Df frost resistance revealed in other IUFRO test sites, where

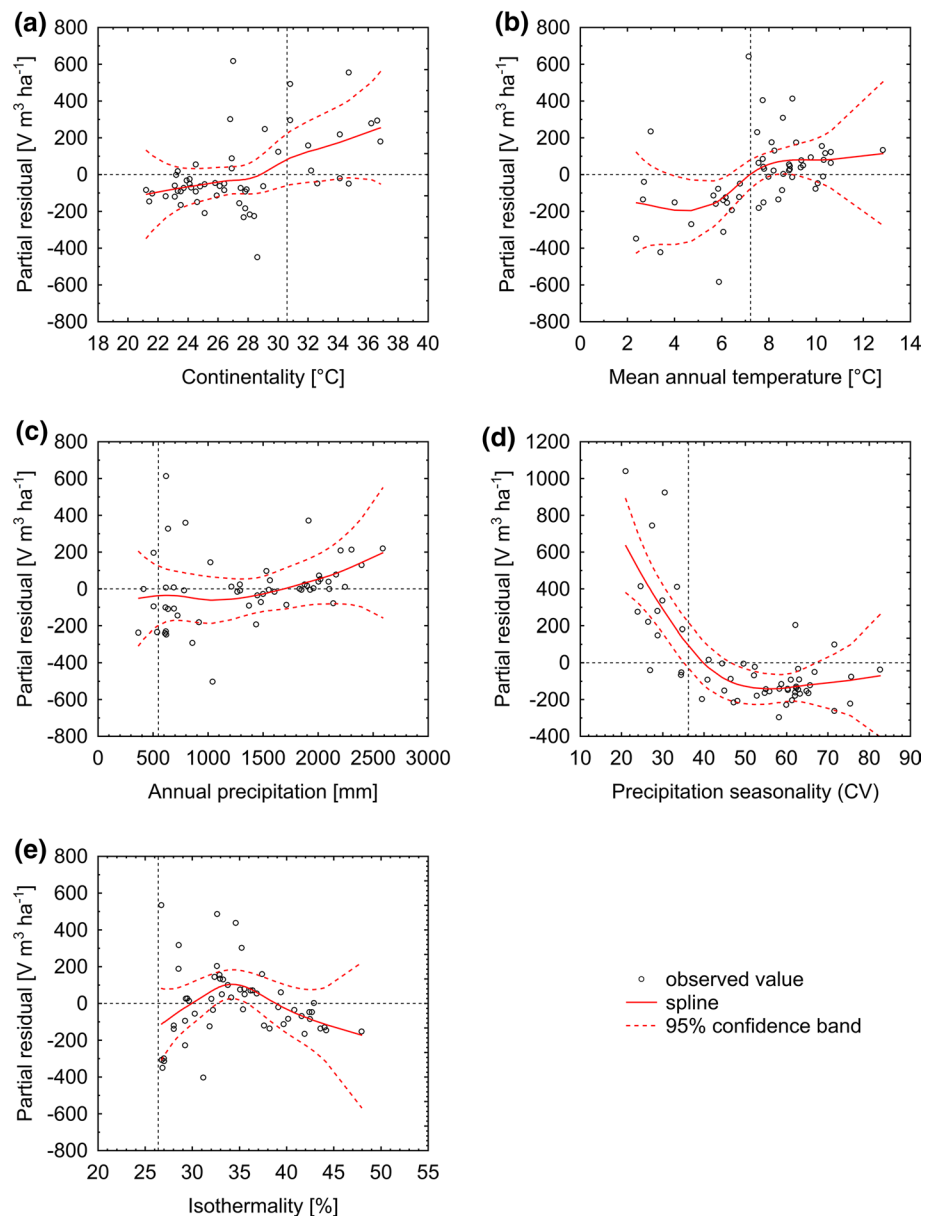
interior populations, especially from BC, were the most resistant to early and winter frosts (Braun and Wolf 2001).

Previous research has shown that a trade-off exists between frost tolerance and growth performance in Df populations. The interior variety typically shows higher frost resistance but lower growth potential when compared to the coastal variety (Rehfeldt 1977; St Clair et al. 2005; Krakowski and Stoehr 2009; Benowicz et al. 2020). However, in our current research, where the most continental conditions among the IUFRO Df test sites in lowland Europe exist, we found that the interior populations showed not only superior frost-resistance, but also superior productivity in a continental climate. Thus, our results provide evidence to support the earlier suggestions by Isaac-Renton et al. (2014), that for the continental climates in Europe, the interior Df provenances are likely to be a more appropriate and a safer choice for reforestation than coastal provenances.

Productivity of Df is one of its greatest advantages (Chylarecki 2004; Krakowski and Stoehr 2009), which has driven worldwide interest in this species. The best performing provenance at our Rudka test site was from White Lake [7-i-S-BC], achieving a stand volume of  $1216 m^3 ha^{-1}$ , with a mean annual increment (MAI) of  $25 m^3 ha^{-1} yr^{-1}$  at age 48. This MAI is higher than the values reported from stands within the natural range of Df in the USA (Acker et al. 1998) and Canada (Isaac-Renton et al. 2020), and at other European sites (Bastien et al. 2013). Df in our experiment exceeded the productivity of almost all native tree species at a similar age occurring in Poland (Jaworski 2004). Contrary to the results obtained in earlier studies, the current work has shown the high productivity potential of Df in the most eastern/continental research location tested in Europe and confirms the potential usefulness of this species for forestry outside the currently recommended planting zones in Poland and Europe (Chylarecki 2004).



**Fig. 9** Spline-curves showing the partial effects of **a** continentality, **b** annual mean temperature, **c** annual precipitation, **d** precipitation seasonality, and **e** isothermality on a volume per ha basis at age 48 years ( $R^2 = 64.2\%$ ). The vertical dotted lines denote climatic conditions at the Rudka test site in eastern Poland



The analysis of growth dynamics in our study revealed that the best performing provenances, i.e. White Lake [7-i-S-BC] and Salmon Arm [6-i-S-BC], maintained their dominant position throughout the experimental period, i.e. in the two time intervals considered. Due to their better adaptability to environmental conditions in the initial phase of tree growth (frost-resistance), they were characterized not only by a higher survival rate but also their annual increment was faster than that of the trees from the other provenances. Over time, with canopy closure in the experimental area, the trees of these two provenances were able to effectively compete for light, water, and nutrients as they developed larger stems and crowns faster than the trees from other provenances. It seems possible that their exceptionally high PAI in the second time interval (2005–2017) resulted from a favourable

combination of their adaptability, plasticity, and the maintenance of their dominant position in the canopy, while trees from some other provenances were gradually overtopped and suppressed. Weaker competitiveness and plasticity of trees seems to have played a role in tree mortality, especially in the second time interval of our study. However, this issue is beyond the scope of the present study and no conclusions should be drawn on this aspect without additional analyses (e.g. dendrochronological study).

The analysis of geographic trends in growth parameters and survival rates at Rudka showed clear relationships with latitude, longitude and elevation of the seedlot provenances. These relationships explained over 80% of the variation in survival and over 77% of the variation in volume per hectare. According to the GAM analysis,

the optimum range of geographic ranges from which Df provenances are recommended for introduction into continental climates in the lowland region of Central Europe is from 50–54°N latitude and < 119°W longitude, with an elevation not higher than 700 m a.s.l.. The longitudinal variation corresponds more to the distance from the ocean, associated with continentality in North America, than to absolute degrees of longitude (Campbell and Sorensen 1978; Rehfeldt et al. 2014). The trend in productivity related to seed source altitude was rather weak in our study compared to the typically steep clines shown previously in Df (Rehfeldt 1989; Rehfeldt et al. 2014). However, the provenances included in our experiment did not represent the whole altitudinal range of the species distribution.

Among the five bioclimatic characteristics of seed origin that explained the largest part of the variation in productivity-related traits in our study, the precipitation seasonality had the highest impact, whereas the MAP, MAT, continentality and isothermality had smaller effects. Similar to our results, the MAP of the origin sites was not a significant factor in models predicting growth performance of Df in Austria and Germany, where even at the driest sites, the coastal Df variety performed well (Chakraborty et al. 2015). However, moisture conditions seem to be important as the summer heat:moisture index was among the most influential factors affecting the projected provenance performance in Chakraborty's et al. studies (Chakraborty et al. 2015, 2016) and, as mentioned, precipitation seasonality was the most important bioclimatic factor in our study. At the Rudka site, years with an annual precipitation higher than 600 mm are rare, and precipitation occurs throughout the year although the largest portion of rainfall occurs during the summer (Fig. 1). In contrast, most of the provenances tested in Rudka originated from the west (coastal) side of the Cascade Mountains in WA (optimal conditions for the Df in its natural range), where the annual precipitation is 1800–2200 mm, with the majority of this precipitation occurring during the winter months (Chylarecki 2004). Thus, with the abundance of precipitation and relatively small temperature amplitudes during the year, the oceanic climate of the western Cordillera is difficult to compare with the climate of eastern Poland, which is moderately cold with prevailing continental conditions (Kondracki 2009). The inferior growth potential of the coastal variety in our study can therefore be explained by an incompatibility in climatic conditions between origin and test site. From the range of climatic variability covered by Df provenances sampled in our study, the climate in BC is most similar to that of eastern Poland. In particular, the continental plateau between the Coastal Range and the Rocky Mountains, where the interior Df provenances from Salmon Arm [6-i-S-BC] and White Lake [7-i-S-BC] originate, and where the climatic conditions are comparable

to our study site, these two provenances performed best at Rudka.

Although our study was not specifically designed to investigate physiological responses to water stress, our findings suggest that even a small amount of precipitation, occurring uniformly during the year (small CV of precipitation seasonality), can provide sufficient resources to support good performance of Df at more continental locations. When taking into account global and regional projections for the direction of climate change and the speed of change as well as the magnitude and frequency of extreme events including droughts and heat events (IPCC, 2013), Df populations from regions with relatively cool winters and arid summers may be most adapted to cope with drought conditions that are expected in the future (Bansal et al. 2015). In light of these findings, it appears that the interior Df variety, which showed better performance at the Rudka site, will be a safer and more profitable choice for eastern Poland under future climate projections. In the context of the recommendations regarding reforestation under projected climate change, it is possible that other Df provenances might grow as well as the interior variety or even better in a new, future climate at the site. However, the results of our study indicate that frost resistance is, and likely will remain, an important factor affecting early survival and success of Df plantations grown in continental climates, which is critical for plantation success. Future climates are projected to be warmer (Collins et al. 2013), but those projections do not preclude the occurrence of extreme weather phenomena, especially the late and early frosts in locations with continental-type climates, and the populations from the interior Df range with superior growth would be desirable for such sites (Chakraborty et al. 2019).

The local landraces which were tested in our study were clearly distinguishable between the interior and coastal types based on survival and biometric characteristics (H and DBH). The landraces of the interior type, located at Wirty [47-i-N-PL], Biedrusko [51-i-N-PL] and Dębno [50-i-N-PL], had significantly higher productivity at Rudka than those originating from the coastal native range. The latter suffered from frost damage at the early stage of the experiment (Burzyński 1990), which resulted in high mortality rates and inferior growth capacity. Yet, not all the landraces of the interior type had satisfactory survival, and the Wirty landrace was clearly superior for both growth and survival. Certainly, stands that were planted with originally introduced seed sources underwent acclimation to the sites, and the non-adapted individuals which died-off did not produce offspring. However, those stands were not previously progeny-tested, thus their value as landrace populations is not known. Our study contributes to closing this knowledge gap. However, as we have no information on the origin of the landrace populations, we also have no knowledge about the

level of genetic variation they represent without additional genomic testing. It may be the case that progeny of some of those stands show poorer adaptive capacity because of the limited genetic variation potentially due to a founder effect. Further studies would need to be conducted to determine the level of genetic variation in the landrace stands and their progeny. Our study showed that the interior Df variety could be successfully planted in eastern Poland, however, performance of this variety was not uniform and any new introductions would need to be fully tested. It should be noted, however, that our results are based on a single test site, and we should be cautious with findings from this study when making reforestation recommendations at a broader scale. More field tests are needed, especially in continental-type climates, to confirm the suitability of interior Df provenances and local landrace populations for consideration in forestry practice. Our findings indicate that the seed base for Df in Poland should be continuously improved and perhaps even enriched with new genetic material from the natural range of this species, taking geographic and climatic criteria into account. Further support should be considered with additional field trials, early greenhouse screening and DNA testing.

## Conclusions

Overall, our results show a significant impact of geographic location and climatic conditions of the seed source origin of Df on survival and growth rate in a continental test site in eastern Poland. It appears that both geographic and climate characteristics should not be treated independently, as geographic location integrates many factors shaping local adaptation, including climate characteristics, phenology, photoperiod length, and angle of solar radiation, all of which affect plant growth. The interior Df variety performed best at our study site, which is in clear contrast to many sites with temperate climates in Europe, where the coastal variety is recommended. Thus, under projected climate change, our study revealed the potential for additional introductions (assisted migration) of Df, especially the interior variety, beyond the current recommended planting zones in Europe. The tested Df provenances did not show sensitivity in their response related to annual precipitation or mean annual temperature, however, they did show sensitivity to precipitation seasonality which implies that seasonal droughts could potentially limit the growth capacity of Df at such sites. Furthermore, the significant effect of late frosts on survival of some provenances, at an early age, indicates that these provenances should be avoided in locations with more continental climates in Europe. Therefore, we suggest that assisted migration programs should consider the limitations imposed by both late frost events and projected increases in

frequency of drought events in guiding future selections. The landraces tested in this single study site showed mixed results as potential seed sources. Our study shows that local landraces in Poland could be enriched with new genetic material from the natural interior Df range of this species, with particular attention being taken as to the geographic location and climate, relative to the deployment area under consideration in more continental climates. Testing of an enriched source population would also benefit forest practitioners in determining site suitability in the future across both Poland and other regions in Europe.

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**Data availability** The datasets generated and/or analysed during the current study can be available on request.

## Declarations

**Conflicts of interest** The authors declare that they have no conflict of interest.

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