

Article

Differences in Growth and Log Quality of Douglas-Fir (*Pseudotsuga menziesii* (Mirb.) Franco) Provenances

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Abstract: Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is a non-native conifer from western North America that was introduced into European forests at the end of the 19th century. Plantations of Douglas-fir in Europe have shown good performance, quality, and resilience to exacerbating climatic conditions. However, all these qualities strongly depend on provenance. A total of 1061 surviving trees of fifteen different Douglas-fir provenances were measured in a Slovenian provenance trial that was established within the framework of the 1966/1967 IUFRO seed collection program. We found significant differences among provenances with respect to survival rate, growth performance, and log quality. The total recorded yield of the 46-year-old stand was 602.9 m³/ha, and the average survival rate was 43%. The correlation of juvenile tree heights in 1985 and their average breast height diameters in 2017 is positive and significant. Based on vitality and diameter, the best performing provenances were *Yelm* and *Cathlamet*. The provenance with the best log quality assessed through branchiness is *Jefferson* (Olympic Peninsula, western Washington). All the most promising provenances for western Slovenia (Central Europe) originate from the low-altitude western coast of Washington (WACO), with the *Cathlamet* provenance showing the best combination of good growth, survival rate, and log quality.

Keywords: coniferous plantation; IUFRO provenance trial; non-native species; variability; growth; branching

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1. Introduction

Climatic fluctuations, along with pests and diseases outbreaks, have a considerable impact on forest ecosystems [1–3]. Reduced water availability caused by extremely warm and dry conditions is expected to become a major threat to the productivity and stability of forests (especially Norway spruce plantations) in Europe in the coming decades [4–9]. Increasing global demand for wood and rising interest in the green economy are likely to lead to changes in forest management [10]. Coping with these challenges will necessitate the new selection of tree species, including economically valuable non-native tree species [1,11,12], with the ability to maintain growth rate in a drier and warmer future climate with more extreme events such as freezing rain, hail, and windthrow [13].

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) has been found to be a very useful species for afforestation and reforestation in Central and Western Europe: it originates from the western part of the United States and Canada and was introduced to Europe in the 19th century [14,15]. Currently, Douglas-fir is one of the most important non-native timber species in Western and Central Europe [12,14,16,17]. It has a high growth potential, even exceeding that of Norway spruce [18]. At the same time, Douglas-fir is a relatively undemanding species that copes well with chronic droughts and exhibits relatively high increment rates even when other conifers do not [19,20].

Douglas-fir currently covers an area of 830,707 ha in Europe [21], and this area is expected to increase [16,22]. This is not surprising given its impressive growth performance. In Germany, Douglas-fir is one of the most productive tree species in terms of growth, economic output, and carbon sequestration [16]. On comparable (but not extreme) sites, Douglas-fir's growth capacity is much higher (15% to 50%) than that of Norway spruce and beech, and even higher (50% to 60% and more) compared to pine and oak [12]. The variation in growth of Douglas-fir in Europe largely (40%–50%) depends on its origin [23]; different races are tested in field experiments. Forestry experts were aware of provenances in early 1910, but in 1967 the most important international IUFRO (International Union of Forest Research Organizations) project was set, aiming to preserve and establish genetic resources for supplying nurseries with best seed material [15]. For provenance tests, parameters that indicate age-related dimensions in the development stage are very desirable. Height growth of Douglas-firs at an early development stage is a good predictor for growth in older stages [24]. However, there are still provenances that show good performance in pole stage but later exhibit a drop in performance [24,25].

In its natural habitat, Douglas-fir grows in an extremely wide range of site conditions and accordingly displays high adaptive genetic variability. These facts are reflected in different flushing dates, susceptibility to late or early frost damage, and susceptibility to different pests and diseases [1]. Coastal Douglas-fir (*P. menziesii* (Mirb.) var. *menziesii*) grows better in Europe than the interior variety (*P. menziesii* (Mirb.) var. *glauca*) and is also more resistant to needle cast (*Rhabdochline pseudotsugae*) [14]. In Germany, the best growth performance has been found in provenances from Oregon, western Washington, and southeastern British Columbia, all originating from elevations of less than 600 m above sea level (a.s.l.) [1,14]. France has the largest number of Douglas-fir plantations at mid-elevation regions, predominating with provenances from lower altitudes (<450 m a.s.l.) of the western side of the Cascade Range [17,26]. A major challenge for European forestry is therefore to target the most appropriate genetic material (provenance) for selected sites under future climatic conditions [1,12,24,27,28].

In addition to growth performance, which is important for timber production, wood properties for pulp production and log quality for wood processing industry are also very important [26,29]. The quality of coniferous wood depends primarily on the number and diameter of knots [30]. Ramicorns on the lower half of the trunk area also have a detrimental effect on log quality [31]. The number of branches primarily depends on genetics, while branch diameter primarily depends on stand density [32], so branch size could be controlled with planting density [1]. Based on branchiness, the best provenances in Europe are those from the coastal areas of Washington, and those that have the worst branching habit are from southwestern Oregon [33]. Most research related with planting density on Douglas-fir log quality was made in young plantations (<25 years old) [32,33]; thus, research results from older Douglas-fir plantations are rare or lacking.

The aim of our study was to test whether Douglas-fir provenances grown in a 46-year-old IUFRO provenance trial in Brkini (Slovenia) differ with respect to tree survival, growth performance, yield, and log quality. We wished to identify the most suitable or promising provenances for the western part of Slovenia (Central Europe). In addition, one of our research goals was to determine whether the better height growth of a certain provenance in the young stage indicates its better diameter growth in the adult stage. This could be useful in evaluating the future potential of young plantations. Conifers generally have a strong and significant height–diameter correlation [34,35], and our further analysis derives from this correlation. The data on the average provenance heights in 1985 were taken from Breznikar (1991) [36]. Our hypothesis was that the superior height growth rates of individual provenances in the young stages are maintained in the following decades and after, expressed with above-average diameter growth.

2. Materials and Methods

2.1. Study Site and Origin of Provenances

Studied Douglas-fir trees are grown in a provenance trial site named Padež I and belong to the forest district of Sežana, Slovenia (45°36'13" N; 14°3'21" E). The climate is inland sub-Mediterranean [37] with an average annual temperature of 10.4 °C, average January temperature of 1.3 °C, and average July temperature of 20.1 °C (period 1980–2010). The average annual rainfall is 1306 mm. Precipitation is fairly favorably distributed within the vegetation period, with a slight dip in July and August (climate data from the meteorological station in Ilirska Bistrica (424 m a.s.l.), 16 km from the study site, reference period 1980–2010 [38]). The study site is at 530–580 m a.s.l., the relief is smooth with 5% outcrops, and the soil is a distric brown soil on non-carbonate flysch and decalcified marl.

The provenance trial is part of an extensive IUFRO program in which seeds from the natural range of Douglas-fir were collected and distributed to 20 European countries [15]. The provenance trial in Slovenia was established in 1971 with the planting of 15 coastal Douglas-fir (*P. menziesii* var. *menziesii*) provenances. The experiment plot was rectangular with an area of 1.56 ha, where 2460 trees of various provenances were planted in rows with 2.5-m spacing. Rows consisted of multiple series of 10 trees per provenance, and there were 11–20 repetitions per provenance, depending on available number of seedlings (Table 1, Figure 1). A protective belt of Douglas-fir trees surrounding the plantation was to prevent edge effects, and provenances were planted in a systematic distribution to exclude environmental factors (small differences in soil, slope). In the establishment phase, the trial was fenced, and planting success was above 90% [39]. Prior to this study, data was collected in 1985 [36], and the trial plantation has never been thinned.

Table 1. Provenances in Padež I trial plot: IUFRO code—international provenance IUFRO code; name—provenance name (nearby city); state—federal state; N (°) and W (°)—geographical coordinates; altitude (m)—altitude in meters above sea level; num. seed—total number of planted seedlings per provenance; num. series—number of repetitions [24,27,36].

IUFRO Code	Name	State	N (°)	W (°)	Altitude (m)	Num. Seed	Num. Series
1028	Merrit	Brit. Kolumbija (BC)	50.07	120.85	870–950	180	18
1059	Perry creek	Washington (WA)	48.05	121.47	600–700	197	20
1060	Clallam, Sequim	Washington (WA)	48.03	123.03	60–90	159	16
1064	Jefferson, Hoh River	Washington (WA)	47.80	123.97	240–245	166	17
1070	Denny creek	Washington (WA)	47.40	121.53	540–550	170	17
1078	Cle Elum	Washington (WA)	47.22	121.12	630–700	179	18
1080	Thurston, Yelm	Washington (WA)	47.02	122.73	60	170	17
1081	Alder Lake	Washington (WA)	46.80	122.28	420–430	161	16
1088	Cowlitz, Castle Rock	Washington (WA)	46.32	122.87	150	160	16
1089	Wahkiakum, Cathlamet	Washington (WA)	46.30	123.27	195–200	160	16
1090	Cougar	Washington (WA)	46.08	122.30	500–550	139	14
1094	Washington, Vernonia	Oregon (OR)	45.77	123.22	210–215	110	11
1101	Waldport	Oregon (OR)	44.40	123.87	60–90	170	17
1102	Upper Soda	Oregon (OR)	44.38	122.20	980–3250	179	17
1104	Brookings	Oregon (OR)	42.12	124.20	300–365	160	16

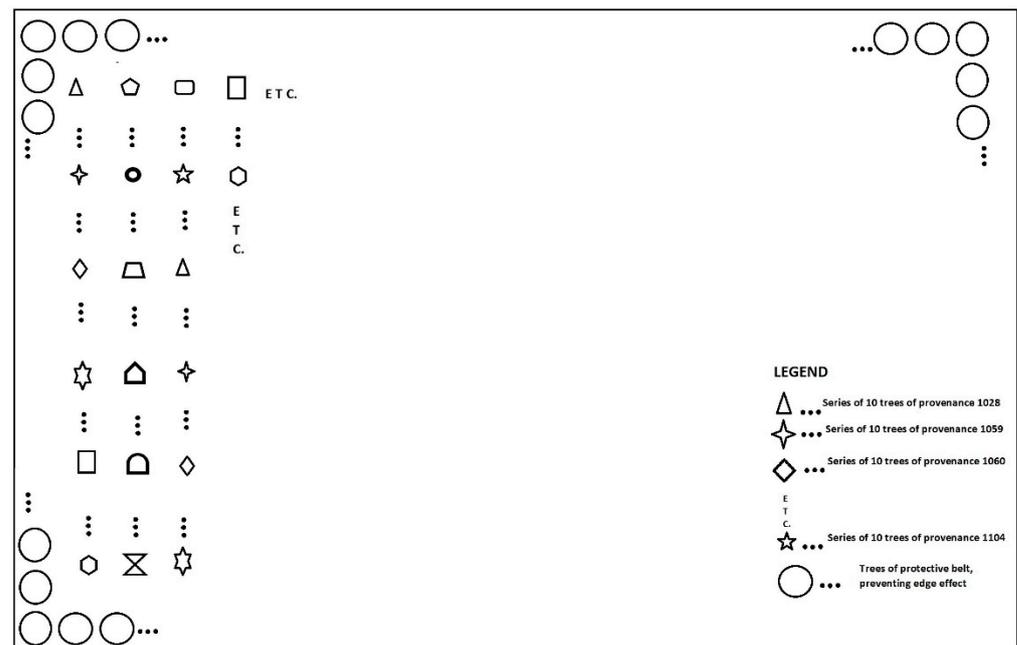


Figure 1. Experimental plot design with legend. The distance between individual trees and rows is 2.5 m.

2.2. Field Measurements

Data was collected in April and May of 2017. We performed measurements on all living Douglas-fir trees. Trunk diameter was measured at breast height ($dbh_{1.3}$, hereafter dbh) and the degree of precision was 1 mm. All trees were classified in vitality classes (3: good vitality, 2: medium vitality, 1: low vitality) according to Leibundgut (1956) [40]. For all trees, several special features that can potentially affect log quality were recorded (multiple trunks and shriveled shoots at a sharp angle (ramicorns)).

We assessed branch number and measured the diameter of branches with small calipers as close as possible to the trunk. All branches with a diameter greater than 8.0 mm that were in a 100–160 cm band above the ground level were measured. The data was used to objectively estimate log quality [32]. Branchiness was not evaluated on all trees but was systematically sampled on the 3rd and 5th live tree in each provenance series. If the number of remaining living trees in a series was less than five, we performed a draw to ensure randomness. Douglas-fir trees with more space for growth (trees along forest trails) were excluded from the analysis of branchiness.

2.3. Statistical Analyses

In the calculations of timber volume, each trunk on multi-trunked trees (forking below breast height) was treated as an autonomous tree. For other analyses (survival, vitality, and dbh), average dbh and average estimates of the vitality of all trunks were used for calculation. Since we were not able to measure tree heights due to the high stand density, for wood stock calculations the 4th tariff class (E4) for even-aged forests were used. Tariff class was determined in forest management plan [41] by the Slovenian Forestry service according to procedure, described in Kotar (2003) [42].

Because certain conditions for homogeneity of variance were not met, a non-parametric Kruskal–Wallis test was used to determine differences among provenances in average dbh and vigor. In the posterior analysis, the Mann–Whitney U-test was used. Due to multiple comparisons, Bonferroni's correction of the critical p -value [43] was performed.

The differences in branchiness at band 100–160 cm above the ground were checked according to the following criteria: the number of branches (NOB), the average diameter

of branches (ADB), the maximum diameter of branches (MDB), and the average diameter of the four thickest branches at breast height (AFB) [32]. The Kruskal–Wallis test was used to test for differences according to individual branchiness criteria, and the pairing between the provenances was done with the Mann–Whitney U-test. When considering the potential impact of provenance and dbh on the number and diameter of branches, an analysis of covariance (ANCOVA) was designed where “provenance” was a fixed factor and dbh was used as a covariate. Growth trend comparisons were tested with the Pearson and Spearman correlation coefficients between the height data from 1985 and diameter data from 2017. All analyzes and computations were performed with IBM SPSS Statistics 25.0 software (IBM Corp.; Armonk, NY, USA), data editing and charts plotting were done using Microsoft office Excel (Microsoft Corp.; Redmond, WA, USA).

3. Results

3.1. Survival Rate, Vitality, and Growth of Provenances

Data analysis showed that the average survival of provenances in the 46-year-old, never thinned, plantation was 43.0% (1061 trees survived out of 2460 planted). The *Denny creek* (1070) and *Cle Elum* (1078) provenances had the highest survival rates (55.9% and 53.6%, respectively) (Table 2). The *Brookings* (1104) provenance from the south coast of Oregon had the lowest survival rate. Total volume according to tariffs was 602.9 m³/ha.

Table 2. Performance of 15 Douglas-fir provenances originating from the west coast of North America (British Columbia (BC), Washington (WA), and Oregon (OR)) and planted in the Slovenian provenance trial. Measurements on survival, ramcorns, vitality, and diameters were conducted on all trees per provenance. * Arithmetic means from ordinal estimates were calculated only for the sake of easier representation and comparison.

	Provenance (IUFRO- Code)	Survival (%) 1985	Survival (%) 2017	Vitality 2017	Height (cm) 1985	Avg. dbh (cm) 2017	SD (dbh)	% of Trees with Ramcorns 2017
BC	1028	71.7	35.0	1.87	513.4	27.0	9.3	15.9
WA	1059	82.2	51.3	2.30	663.3	32.7	11.0	8.9
	1060	76.1	46.5	2.20	602.1	30.0	10.9	24.3
	1064	67.5	44.6	2.16	595.8	28.6	9.8	13.5
	1070	83.5	55.9	2.25	638.8	31.1	9.7	12.6
	1078	88.3	53.6	2.04	638.3	29.3	8.8	7.3
	1080	77.6	40.6	2.49	591.3	36.1	10.5	14.5
	1081	61.5	31.1	2.18	567.0	31.1	11.6	12.0
	1088	71.3	41.3	2.23	576.9	31.2	10.7	9.1
	1089	75.6	47.5	2.37	651.9	34.1	10.6	9.2
	1090	70.5	44.6	2.24	654.7	32.4	11.9	6.5
OR	1094	57.3	39.1	2.19	615.1	30.8	10.3	2.3
	1101	64.1	41.8	2.26	594.0	31.5	11.0	18.3
	1102	68.2	40.2	2.07	592.0	30.4	9.3	6.9
	1104	48.1	30.6	2.25	573.6	31.7	12.7	12.2
	average *	70.9	43.0	2.21	604.5	31.2	10.4	11.6

With the Kruskal–Wallis test, we confirmed the effect of provenance on average dbh ($H(15) = 40.165, p < 0.001$). *Yelm* (1080) had the highest average dbh (36.1 cm), significantly differing from most of the other provenances (Table A1). In contrast, *Merritt* (1028) had the lowest average dbh (27.0 cm), also significantly differing from most of the other provenances.

The Kruskal–Wallis test was also used to confirm the effect of provenance on vitality ($H(15) = 31.242, p < 0.01$). The most vital provenance was *Yelm* (1080) with an average grade of 2.49, followed by *Cathlamet* (1089) and *Perry Creek* (1059) with grades of 2.37 and

2.30, respectively. The *Merritt* (1028) provenance had the lowest vitality with a grade of 1.87. The Spearman correlation of vitality with average dbh was significant ($p < 0.01$) and high ($r_s = 0.873$).

3.2. Does Height Growth in Youth Indicate Greater Age-Related Diameter?

Correlation coefficients (Pearson and Spearman) $r_p = 0.973$ and $r_s = 0.941$ (both significant ($p < 0.01$)) between tree heights in 1985 and average dbh in 2017 confirmed a similar growth trend for individual provenances in the period 1985–2017. This is also illustrated in Figure 2, where provenances with the highest average tree heights in 1985 dominate with the highest average dbh in 2017. The *Yelm* (1080) provenance deviates from this trend; its average dbh in 2017 was above average, while in 1985 its average height was merely average.

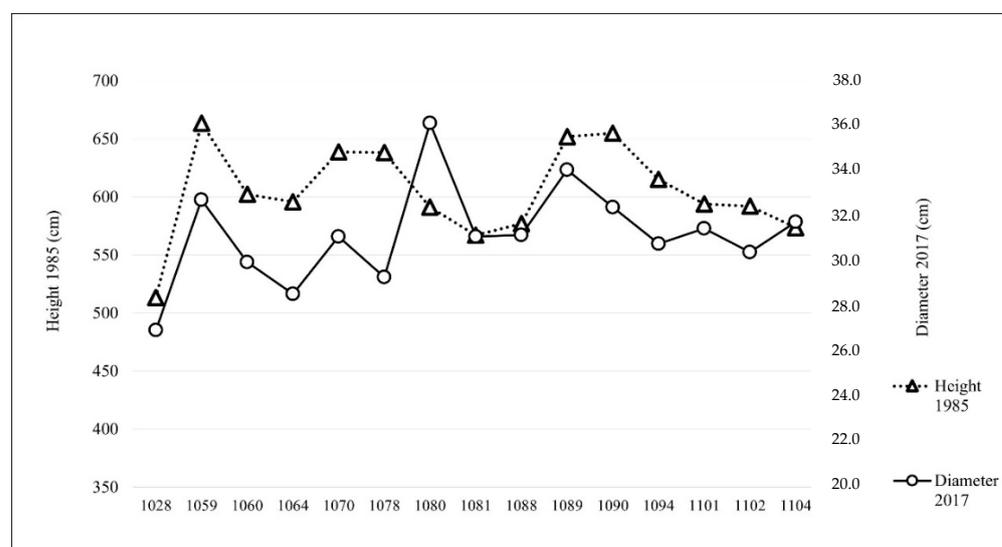


Figure 2. Data on average tree heights in 1985 and average diameter at breast height (dbh) in 2017. See Table 1 for provenance names.

3.3. Differences in Log Quality among Provenances

We found statistically significant differences among provenances with respect to all four measured parameters of branchiness (Table 3). The average number of branches per tree (NOB) was between 9.4 and 12.4, and the average diameter of branches (ADB) was 14.8 to 16.9 mm (Figure 3). The diameter of the thickest branch (MDB) ranged from 31 to 51 mm, while the average diameter of the thickest four branches (AFB) was 17.8–22.4 mm. *Jefferson* (1064) had the lowest number of branches as well as the thinnest branches, while *Cle Elum* (1078) had the largest number of branches. *Yelm* (1080) had the thickest branches accordingly (AFB in ADB) while *Waldport* (1101) had thickest branch (MDB) overall (Figure 3). Ramicorns appeared on 11.6% of trees on average, with *Clallam* (1060) having the share of ramicorns that was the highest at 24.3% (Table 2).

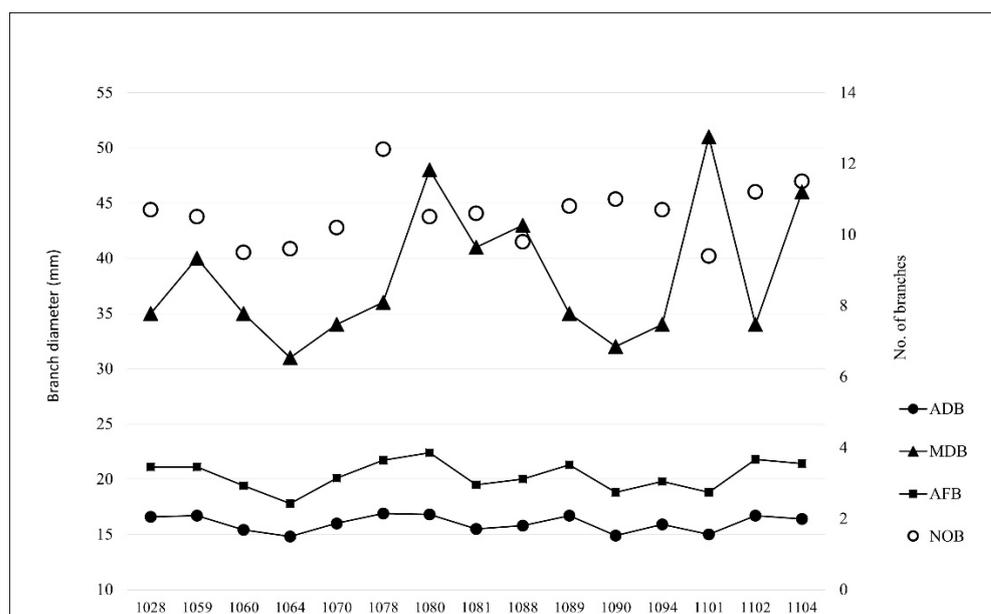


Figure 3. Combined graph of branch criteria, representing the mean values for the individual characteristics studied. See Table 1 for provenance names.

The analysis of covariance showed that the covariate, dbh, was significantly related to the number of the branches, $F = 7.95$, $p < 0.01$. Moreover, a positive value of b for the covariate ($b = 0.041$, $p < 0.01$) means that the number of branches increases with dbh. However, provenance also had a significant effect on the number of branches after controlling for the effect of dbh, $F = 2.21$, $p < 0.01$. Provenance and dbh also had a significant effect on the other studied traits (Table 3).

Table 3. Results of the ANCOVA test. F -values and significance level are shown for provenance as a main factor and dbh as a covariate (b -value and its significance refers to the covariate).

	Provenance	sig.	Covariate dbh	sig.	b	sig.
Number of branches (NOB)	$F = 2.21$	0.007	$F = 7.95$	0.005	0.041	0.005
Average diameter of branches (ADB)	$F = 2.27$	0.005	$F = 159.76$	0.000	0.160	0.000
Maximum diameter of branch (MDB)	$F = 1.85$	0.030	$F = 164.60$	0.000	0.305	0.000
Average diameter of 4 thickest branches (AFB)	$F = 2.63$	0.001	$F = 177.50$	0.000	0.257	0.000

4. Discussion

Our analysis and some other foreign studies from Serbia, the Netherlands, and Bulgaria similarly confirm differences in growth among provenances [14,24,44–46]. In our experiment, *Yelm* (1080) showed the best growth performance, it had the largest average dbh, and performed well against most other provenances (Table 2). *Cathlamet* (1089) and *Perry Creek* (1059) also exhibited large average dbh.

After 46 years, the growing stock of the Douglas-fir provenance trial was 602.9 m³/ha, and the average dbh was 31.2 cm, which is comparable to other studies (e.g., 30.5 cm after 41 years) [24]. In comparable site conditions, other coniferous tree species in such stand type (coniferous plantations on silicate) have a comparable annual increment to Douglas-fir [41]. Average survival at pole stage is comparable with other studies [24].

All provenances in our provenance trial with above-average dbh originated from a lower or (in one case) similar altitude to that of the Padež I trial site (580 m a.s.l.). All provenances with above-average growth performance and superb vitality in the experimental trial originated from the coastal range of Washington (WACO region; [33]), which was previously known to be the most suitable provenance source region for plantation establishment in Europe for sites not experiencing a strong continental climate [14,24,44–

47]. Guidelines for provenance selection in Germany recommend coastal subspecies (*P. menziesii* var. *menziesii*) from an altitude of up to 600 m a.s.l. [12,14,33,48]. On the other hand, coastal provenances from Oregon and Northern California are better suited to a dry climate and are thus usually recommended for drier parts of Europe, such as Apennines (Italy) [14]. Recent findings have revealed that several old Douglas-fir stands in Austria originated from areas outside the recommended regions (e.g., Northern California), indicating that additional seed sources may be suitable for Douglas-fir in Central Europe [28]. The provenance with the lowest average dbh in our trial was *Merrit* (1028), which originates from higher altitudes and latitudes in British Columbia; other provenances from these areas also grow poorly in Serbia [44] and Eastern Austria [49]. In contrast, in northern countries (e.g., the Netherlands), provenances from higher latitudes grow better, and growth decreases with decreasing geographical latitude of origin [24]. Over all provenance trials, breeding programs, and planned afforestation in the past, current mature Douglas-fir stands in Europe maintain high genetic diversity, which can (under certain conditions) benefit adaptive forest management under climate change [50]. It is also possible that the future suitability of certain provenances changes so that the coastal provenances from current altitudes that are currently optimal for Europe could be replaced with southern range or more drought-tolerant interior subspecies in the future [27,51,52]. While some models predict an improvement in conditions for Douglas-fir growth in the Alps, others predict a 10%–36% decrease in growth on today's optimal sites [53]. It is also important to consider the effect of climate change on Douglas-fir pathogens. Higher temperatures and moisture levels in spring could promote pathogenic fungi such as *Rhabdocline pseudotsugae* and *Nothophaeocryptopus gaeumannii*, which can infect resistant provenances, resulting in poor growth or death of a Douglas-fir tree [1].

Among the provenances themselves, and even among the descendants of a single Douglas-fir tree, there are differences in the rhythm of growth within the lifespan of a tree [54]. We compared growth trends of the individual provenances for the period from 1985 to 2017 and found a strong correlation between tree heights in 1985 and their average dbh in 2017. Similar results were obtained in the Netherlands, where most provenances remained in the same ranking after a 24-year period [24]. Similarly, juvenile growth was shown to have a positive and significant correlation with the heights [55]. A significant correlation indicates that juvenile growth could be a good predictor or indicator of future radial growth. This strong correlation suggests that it is possible to make a satisfactory selection in younger stages. Despite being a relatively long-lived species, commonly reaching an age of 750 years [48], coastal Douglas-fir exhibits rapid juvenile growth and reaches a dimension suitable for economic exploitation at a young age. Consequently, Douglas-fir trunks are full of dead and living branches, which affect log quality. Douglas-fir is generally known as a species with poor self-pruning ability, with provenance having some influence on branch characteristics [1]. Our analysis confirmed an influence of a provenance on the number and diameter of branches, which was also found in experimental plots in the species "native" range [32] and in provenance trials in the UK [33]. Regarding branch number and size, *Jefferson* (1064) was shown as the best, having small number and small diameter of branch, but the *Yelm* (1080) contrarily having the worst (Figure 3). On the other hand, thick branches and the presence of lateral shoots (ramicorns) are common issues for the most productive trees and provenances [48]. *Brookings* (1104) originates from the southern shores of Oregon (SOCO region) and has a poor branching habit, but the remaining coastal provenances from Washington (WACO), such as *Clallam* (1060), *Jefferson* (1064), and *Cathlamet* (1089), show below-average branchiness, which corresponds to other findings [33]. The number of branches primarily depends on genetics, while the diameter of branches primarily depends on planting density [32]. Spacing can be used to control branch size; at a planting density of 1000 trees per ha, branch diameters are thicker than 40 mm. A density of 1000–2000 trees per ha is recommended for smaller branch diameters [56], but even at a density of 4000 trees per ha, self-pruning never results in branch-free timber [1]. Therefore, production of high-quality logs in a short period of

time (up to 80 years) is only possible with artificial pruning [1,12,56]. In our case, the trial plantation was never thinned or pruned, and the trees are heavily branched. The quality of coniferous logs depends on the straightness and shape of the trunk, but it primarily depends on the abundance and diameter of knots. According to log and product grading rules, all logs in the trial would be classified in the C and D quality classes, because of knots larger than 50 mm [30,57]. Quality is obviously very poor at this age, but we expect that quality will start to improve with increasing age. Side shoots (ramicorns) also detract from log quality, as they result in twisted fiber and undesirable trunk shapes. However, ramicorn formation depends more on ecological factors other than genetics [58], including site productivity, distance to the coast [59], and frost and pest damage [60]. In our case, ramicorns were not a decisive factor in the poor log quality grades.

5. Conclusions

In this study, we analyzed a provenance trial established within the IUFRO framework in 1970. We confirmed significant differences in growth performance among analyzed Douglas-fir provenances. In general, provenances from the WACO region exhibited better growth performance than the others. We confirmed that juvenile height is correlated to age-related radial growth. Significant differences among provenances in branching habit were also found. Despite dense planting and no thinnings, our results and field observations showed poor self-pruning at 46 years, and consequently low log quality. We were unable to identify the best provenance based on both high growth rate and superior branching habit. Under current conditions, disregarding predicted future climate change and invasive alien pest species threats, the *Cathlamet* provenance of Douglas-fir could be an optimal choice.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. Matrix of pair comparisons of provenances average dbh with the Mann–Whitney U-test (p values). Significance levels are adjusted using sequential Bonferroni according to Rice (1989)49 (** $0.001 < p < 0.01$; *** $p < 0.001$). See Table 1 for provenance names.

Provenance	1028	1059	1060	1064	1070	1078	1080	1081	1088	1089	1090	1094	1101	1102	1104
1028		0.001	0.107	0.329	0.007	0.074	1.4×10^{-6} ***	0.064	0.026	9.6×10^{-5} **	0.007	0.051	0.018	0.029	0.034
1059				0.019	0.378	0.049	0.043	0.437	0.402	0.406	0.888	0.386	0.468	0.199	0.732
1060				0.509	0.461	0.78	0.001	0.539	0.515	0.025	0.248	0.665	0.432	0.801	0.387
1064					0.129	0.606	6.5×10^{-5} **	0.246	0.215	0.002	0.071	0.311	0.137	0.292	0.138
1070						0.235	0.003	0.98	0.973	0.069	0.558	0.847	0.961	0.555	0.729
1078							6.3×10^{-5} **	0.364	0.294	0.003	0.119	0.493	0.289	0.679	0.254

1080	0.026	0.009	0.273	0.070	0.016	0.013	0.001	0.074
1081		0.850	0.180	0.606	0.939	0.858	0.783	0.774
1088			0.091	0.559	0.901	0.894	0.575	0.682
1089				0.363	0.113	0.130	0.037	0.381
1090					0.496	0.629	0.305	0.791
1094						0.792	0.844	0.713
1101							0.557	0.928
1102								0.566
1104								

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