Effects of needle cast diseases on the growth of a 33-year-old Douglas-fir provenance plantation in northwestern Bulgaria

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Abstract

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In this study, the effects of defoliation caused by fungal pathogens on the tree vitality and growth of a 33-year old Douglas-fir (*Pseudotsuga menziesii)* provenance plantation in northwestern Bulgaria was presented. The results of the conducted surveys in 2011 and 2020 showed that there were significant differences between the individual provenances of Douglas-fir concerning their susceptibility to the needle cast diseases, caused by the fungal pathogens *Rhabdocline pseudotsugae* and *Phaeucryptopus gaeumannii*. The extent of damage, expressed as the amount of Douglas-fir needles cast, varied among provenance groups in individual years. A serious degree of defoliation was assessed among all continental provenances. In 2011, all examined trees from the group of continental provenances had severe symptoms of the needle cast disease. In 71.5% of them, the defoliation of the crowns was over 25% – moderately to severely affected. The average degree of defoliation varied from 18.3% (32 Warm Springs) to 89.3% (55 Alamogordo). In 2020, severe defoliation was found among all continental provenances. Both fungal pathogens were found as causes of the defoliation of 64.3% of the trees. The growth indicators: average height, average diameter at breast height, average height- and diameter increment for survived provenances in 2011 (at age 24) and 2020 (at age 33) were evaluated. The loss of needles and the reduced physiological function of the trees affected their vitality in the following years. Relationships between the average current annual height and diameter increment by provenance groups for 2003–2011 and 2011–2020 were calculated. It was found that with an increase in the degree of defoliation, the height and diameter increment of the provenances decreases.

Keywords

fungal pathogens, *Phaeucryptopus gaeumannii*, *Pseudotsuga menziesii*, *Rhabdocline pseudotsugae*, tree growth, vitality

Introduction

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) have been a widely used non-native coniferous tree species in the European forests. The species was first introduced to Europe as an ornamental tree in arboreta and parks by the Scottish botanist David Douglas in 1827. From the end of the 19th century it was planted at a progressive rate in the forests of various European countries due to its rapid growth and high productivity (Krumm and Vítková, 2016). Douglas-fir plantations are currently growing on an area of ca. 823,000 ha representing 0.4% of the total European forests (van Loo and Dobrowolska, 2019).

Numerous Douglas-fir provenance plantations were

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established in the 20th century in most European countries (Lavender and Hermann, 2014). The importance of provenance selection from the native range, combined with suitable site assessments, are necessary conditions for achieving high productivity rates and ensuring better adaptive capacity (Hintsteiner et al., 2018). In Germany, the provenances from the northwestern area of Washington are characterized by the highest growth and survival, and the ones from mainland British Columbia show moderate growth (Braun, 1985). In Denmark, provenances from the coastal regions of British Columbia and Washington were found to be the most promising for successful planting in the country (Larsen and Kromann, 1983). The most suitable for the Netherlands are those from western Washington and southwestern British Columbia (Lavender and Hermann, 2014), and from the coast of southwestern Washington, northwestern Oregon, and northern coastal California are particularly well adapted to Italian conditions (Bastien et al., 2013). Numerous provenance tests of Douglas-fir have been established in France that are recommended as suitable for different regions of the country (Bastien et al., 1988). Provenances from the coast of northern, central and southern Washington are recommended for Ireland (Lally and Thompson, 1998), and for Bosnia and Herzegovina – those from northern Oregon, Washington and Vancouver Island (Ballian et al., 2003). For Austria, those from the Western Cascade Mountains in Washington State and the southern parts of Mount Olympia show the best growth performance (Bastien et al., 2013).

Provenance tests with regard to establishing the most suitable provenances for forest afforestation in Bulgaria began in 1987. Seed sources of 55 provenances from 20 seed zones of Oregon, Washington, Montana, Arizona and New Mexico states were delivered from the National seed laboratory for tree species of the USA to the Forest Research Institute in Sofia (Popov, 1991). Seedlings were planted in six provenance tests in different localities in the country – Arboretum of Forest Research Institute (FRI) in Sofia, State Forest Enterprises (SFE) Kostenets, Kyustendil, Lesidren, Zlatograd, and Training and Experimental Forest Range (TEFR) Petrohan (Popov, 2014a). Growth capacity, biomass productivity, tolerance to abiotic and biotic factors of the 55 different provenances were studied in the period 1990–2014 (Georgieva, 2009; Petkova, 2011; Petkova et al., 2014; Popov, 1991, 2014a, b).

Two needle cast diseases caused by the ascomycetous fungal pathogens *Rhabdocline pseudotsugae* Sydow and *Phaeocryptopus gaeumannii* (Rohde) Petr. recently became a severe threat to Central European Douglas-fir stands (Samek et al., 2023). Rhabdocline needle cast has been widespread both in the natural range of Douglas-fir and in the countries where the species was introduced (Boyce, 1961; Stephan, 1973; Butin, 1995; Georgieva, 2009; Samek et al., 2023). In Bulgaria damage of *R. pseudotsugae* was established for the first time in 1977 (Rossnev, 1978a). It was found that all varieties of *P. menziesii* – *P. menziesii* var. *viridis*, *glauca* and *caesia*, suffered from this disease, but *P. menziesii* var. *viridis* was proved to be the most resistant variety (Rossnev, 1978a).

Swiss needle cast disease, caused by the fungal pathogen *P. gaeumannii* was observed in Douglas-fir plantations in Switzerland as early as 1925 (Gaeumann, 1930) and were subsequently reported from other European countries (Boyce, 1940) and from New Zealand and Australia (Beekhuis, 1978; Hood, 1997). In Bulgaria, the disease was recorded for the first time in 1986 (Rossnev, 1987b). The rate of susceptibility of 54 Douglas-fir provenances to the needle cast disease caused by *P. gaeumannii* was studied in the period 2004–2007 (Georgieva and Rosnev, 2008; Georgieva, 2009).

With regard to defoliation, *P. gaeumannii* is the most critical fungal pathogen, responsible for a substantial loss in growth increment in a number of Douglas-fir stands in the native range in North America (Hansen et al., 2000) and also in its introduced range in Europe (Petkova et al., 2014) and New Zealand (Knowles et al., 2001). Defoliation has an effect on forest structure and stand development. At single-tree level the defoliation affects the condition, causing a significant reduction of timber production (Piper et al., 2015). In particular, tree defoliation can result in growth loss (Naidoo and Lechowicz, 2001), reduced root biomass production (Thomas et al., 2002), and increased tree mortality compared to non-outbreak situations (Elling et al., 2007). Tree mortality depends on the frequency, intensity, duration, and combination of defoliation, the vitality status of the infested trees, and biotic or abiotic stresses. Severe defoliation as a stress factor directly affects the photosynthetic processes and indirectly reduces stem growth (Dobbertin, 2005).

The vitality of the trees is one of the most important indicators of forest health condition (Innes, 1993). The effect of fungal pathogens *R. pseudotsugae* and *P. gaeumannii* on the growth and vitality of 54 Douglas-fir provenances at the age of 24 was analysed in the provenance test planted on the territory of the TEFR Petrohan, northwestern Bulgaria (Petkova et al., 2014). At that age, the provenances Newhalem, Darrington and Idanha from the Western Cascade Mountains were characterised with the fastest growth and highest productivity. They showed low susceptibility rates to the needle cast diseases. The continental provenances Greenwood and Keremeos of Washington state, Whitefish of Montana, Bates and Canyon City of eastern Oregon, and Alamogordo of New Mexico were determined as the most susceptible to the pathogens. They showed the slowest growth and the lowest productivity.

The aim of this study was to evaluate tree growth, vitality, and susceptibility to the fungal pathogens, causing needle cast diseases on trees in a 33-year old Douglas-fir provenance test planted in the TEFR Petrohan, Northwestern Bulgaria.

Materials and methods

A provenance test with 54 North American Douglas-fir provenances was planted on the territory of the TEFR Petrohan in the spring of 1990 (Petkova et al., 2014). The plantation is located in the lower part of the northern slopes of the Western Balkan range. It was situated at a flat terrain

Table 1. Geographical data for 30 Douglas-fir provenances planted at the Training and Experimental Forest Range Petrohan (in 2020)

Provenance group	Provenance number	Seed zone	Provenance name	Geographical coordinates N	W	Altitude (m)	Number of trees
			Continental				
New Mexico	55	840	Alamogordo	33.0	105.8	750	4
Washington	1	612	Greenwood	49.0	119.0	1,350	11
	2	600	Keremeos	49.0	120.0	750	23
East Cascade Mountains Oregon	16	661	Parkdale	45.5	121.5	1,350	16
	17	661	Parkdale	45.5	121.5	1,200	19
	18	661	Parkdale	45.5	121.5	1,050	16
	33	662	Warm Springs	45.0	121.5	667	21
	32	662	Warm Springs	45.0	122.0	900	14
	47	681	Crescent	43.3	121.8	1,650	11
	48	681	Crescent	43.3	122.0	1,500	14
East Oregon	36	892	Canyon City	44.5	119.0	1,350	17
Coastal Mountains South Oregon	49	501	Crater Lake	42.7	122.5	1,200	16
	50	501	Medford	42.5	122.5	1,050	16
	51	502	Medford	42.6	122.8	900	17
			Western Cascade Mountains				
Washington	9	411	Monroe	47.8	121.3	525	19
Oregon	24	452	Idanha	45.0	122.0	1,050	16
	25	452	Idanha	45.0	122.0	1,200	19
	26	452	Idanha	45.0	122.0	1,050	17
	30	452	Idanha	45.0	122.0	750	14
	31	452	Idanha	45.0	122.0	750	12
	40	472	Oakridge	44.0	122.0	1,667	14
	41	472	Oakridge	44.0	122.0	1,500	12
	46	472	Oakridge	43.8	122.5	1,500	14
	39	473	Santiam Pass	44.3	121.8	1,500	10
	42	473	Oakridge	44.0	122.0	1,333	18
	43	482	Oakridge	44.0	122.0	900	16
			East Coast				
Washington	10	222	Bremerton	47.7	123.0	600	11
Oregon	34	53	Toledo	44.6	123.8	150	18
	52	82	Brookings	42.0	124.5	833	11
	53	82	Brookings	42.0	124.5	677	11

with the exposure to east, latitude of 43°14’N and longitude of 23°09’E, altitude of 623 m. The soil is Orthic Luvisol (FAO), mixed sandy and clay, slightly stony and very deep, medium rich to rich. The climate in the region is temperate with an average annual temperature of 10.2 °C and precipitation of 1,004 mm. The duration of the vegetation period is about 6 to 6.5 months.

In the winter seasons of 2015 and 2016, and in the spring of 2018, a strong windstorm caused damage to the Douglas-fir trees of twenty four provenances. The identities and geographic characteristics of the remaining 30 provenances in the natural area were summarised in Table 1. According to the regional distribution, the provenances were divided in three main groups: continental (14), the Western Cascade Mountains (12), and coastal (4).

In October 2020, the diameter at breast height and height of trees were measured. The degree of crown defoliation of studied trees was evaluated in 2011 and 2020 regardless of the cause of foliage loss. Tree health condition was categorised according to Eichhorn et al. (2016): healthy (0–10% defoliation); slight defoliation (>10–25%); moderate defoliation (>25–60%); severe defoliation (>60<100%) and dead (100%). The trees with defoliation up to 25% are considered ‘undamaged’. The average defoliation of each provenance was expressed per provenance level as the arithmetic mean of the values of defoliation of 350 trees in 2011 and of 215 trees in 2020.

A univariate linear regression model was created to establish a relationship between the average current annual height- and diameter increment of the groups of Douglas-fir provenances and the defoliation rate (Molle, 2012). The validity of the model regarding the constant variance was proven by the Breush-Pagan test (Zeileis and Hothorn, 2002), the null hypothesis was accepted because the variance was constant. The model was applied to the three groups of surviving provenances for two periods – from 2003 to 2011 and from 2011 to 2020.

Results and discussion

The results of the conducted surveys in 2011 and 2020 showed that there were significant differences between the individual provenances of Douglas-fir in relation to their susceptibility to the Rhabdocline needle cast caused by the fungal pathogen *R. pseudotsugae* and Swiss needle cast caused by *P. gaeumannii*. The extent of damage, expressed as the amount of Douglas-fir needle defoliation, varied among provenance groups in individual years. In 2011, all examined trees from the group of continental provenances had severe symptoms of the needle cast disease, and in 71.5% of them, the crown defoliation was over 25% (moderately to severely affected). The average degree of defoliation varied between 18.3% (32 Warm Springs) to 89.3% (55 Alamogordo) (Table 2).

In 2020, severe defoliation was found among all continental provenances. Both fungal pathogens were found as defoliation causers for 64.3% of the trees from the continental provenances. Premature needle cast began with the older, more severely infected needles. Complete defoliation of all needles was observed in the most severely infected trees. In a nine-year period, there was an increase in tree crown defoliation in all continental provenances. The average degree of defoliation varied from 26.9% (16 Parkdale) to 90% (55 Alamogordo) as a result of the infection by the fungi *R. pseudotsugae* and *P. gaeumannii*. The most heavily damaged were all trees from provenance 55 Alamogordo (New Mexico) with 90% mean defoliation, followed by trees of 36 Canyon City (Oregon) – 77.6% and 1 Greenwood (Washington) – 64.5% (Table 2).

In 2020, it was established that 38.6% of the trees from continental provenances were dead due to the infection caused by the fungal pathogens and damage by the windfalls in 2015–2018.

The loss of needles and the reduced physiological function of the trees affected their vitality in the following years. The total defoliation assessment of trees of continental provenances, carried out in 2011, showed a gradual transition of trees from middle defoliated to severe defoliated (Table 2).

In 2011, all trees of the provenances from the Western Cascade Mountains had needle cast disease symptoms caused by the pathogen *P. gaeumannii*, but no mass defoliation was found. Deterioration of tree health from the provenances of western slopes of the Cascade Mountains was established in 2020, when 89.1% of trees had 30–90%

Table 2. Health status of Douglas-fir trees in provenances at the Training and Experimental Forest Range

Provenance group	Provenance number	Provenance name	Percent of defoliation min-max (mean value) 2011	2020	Pathogens
			Continental		
New Mexico	55	Alamogordo	80–90 (89.3)	90–90 (90.0)	*P. gaeumannii, R. pseudotsugae*
	1	Greenwood	20–70 (42.9)	30–90 (64.5)	*P. gaeumannii, R. pseudotsugae*
	2	Keremeos	50–90 (42.9)	30–90 (55.0)	*P. gaeumannii, R. pseudotsugae*
	16	Parkdale	10–30 (18.7)	20–60 (26.9)	*P. gaeumannii, R. pseudotsugae*
	17	Parkdale	10–50 (23.3)	20–50 (33.7)	*P. gaeumannii, R. pseudotsugae*
	18	Parkdale	20–70 (26.2)	20–90 (41.2)	*P. gaeumannii, R. pseudotsugae*
	33	Warm Springs	20–40 (26.3)	30–90 (48.1)	*P. gaeumannii, R. pseudotsugae*
	32	Warm Springs	10–30 (18.3)	20–70 (40.0)	*P. gaeumannii, R. pseudotsugae*
	47	Crescent	10–40 (21.1)	20–60 (40.1)	*P. gaeumannii*
	48	Crescent	10–50 (30.0)	30–70 (46.4)	*P. gaeumannii*
East Oregon	36	Canyon City	30–90 (70.0)	60–90 (77.6)	*P. gaeumannii, R. pseudotsugae*
Coastal Mountains	49	Crater Lake	20–50 (31.1)	30–70 (43.8)	*P. gaeumannii*
South Oregon	50	Medford	10–60 (21.3)	30–70 (51.3)	*P. gaeumannii*
	51	Medford	10–50 (25.9)	20–70 (38.8)	*P. gaeumannii*
			Western Cascade Mountains		
Washington	9	Monroe	20–50 (30.0)	20–80 (42.6)	*P. gaeumannii*
Oregon	24	Idanha	10–40 (23.8)	20–50 (35.9)	*P. gaeumannii*
	25	Idanha	10–40 (27.3)	30–90 (47.3)	*P. gaeumannii*
	26	Idanha	10–40 (21.8)	20–90 (38.2)	*P. gaeumannii*
	30	Idanha	10–80 (25.6)	20–70 (43.8)	*P. gaeumannii*
	31	Idanha	10–90 (38.0)	30–90 (45.4)	*P. gaeumannii*
	40	Oakridge	20–40 (27.7)	30–70 (45.3)	*P. gaeumannii*
	41	Oakridge	20–40 (26.3)	20–40 (30.9)	*P. gaeumannii*
	46	Oakridge	10–30 (19.0)	30–70 (51.4)	*P. gaeumannii*
	39	Santiam Pass	10–40 (26.7)	30–60 (44.0)	*P. gaeumannii*
	42	Oakridge	20–70 (30.7)	30–80 (44.4)	*P. gaeumannii*
	43	Oakridge	10–40 (20.0)	30–80 (45.3)	*P. gaeumannii*
			East Coast		
Washington	10	Bremerton	10–30 (22.2)	20–50 (34.5)	*P. gaeumannii*
Oregon	34	Toledo	20–90 (31.5)	30–100 (51.1)	*P. gaeumannii*
	52	Brookings	20–50 (24.5)	20–50 (34.5)	*P. gaeumannii*
	53	Brookings	20–40 (23.6)	30–60 (44.0)	*P. gaeumannii*

defoliation (Table 2). Among them, 12.9% were severely damaged with defoliation 70–90%. Trees from provenance 25 Idanha, Oregon (mean value of defoliation – 47.3%) and 46 Oakridge (mean value of defoliation – 51.4%) showed the highest sensitivity.

Swiss needle cast was found in all provenances from the eastern coastal area (Table 2). In 2011, *P. gaeumannii* was found on the needles of all trees surveyed, but slight crown defoliation was reported in 83.6% of them. During the period 2012–2020, there was a deterioration in the health status of trees from these areas. In 2020, 7.8% of the assessed trees were most affected, with crown defoliation between 70% (severely damaged) and 100% (dead).

Tree growth processes can be ranked by order of importance in foliage growth, root growth, bud growth, storage tissue growth, stem growth, growth of defence compounds and reproductive growth. Under stress photosynthesis is reduced and carbon allocation is altered. Stem growth may be reduced early on as it is not directly vital to the tree.

Actual growth must be compared against a reference growth, such as the growth of trees without the presumed stress, the growth of presumed healthy trees, the growth in a presumed stress-free period or the expected growth derived from models.

The growth indicators: average height, average diameter at breast height, average height- and diameter increment for survived provenances in 2011 (at age 24) and in 2020 (at age 33), were presented in Table 3. From the data, a change in increment over the 9-year period can be established. From the data on defoliation in Table 2, it can be seen that it deepened over the 9-year period. It is logical that the increase in defoliation percentage will also affect the height- and diameter increment. Retention and decline in height- and diameter increment is mainly observed in continental provenances (Table 3). In them, the beginning of infection by the fungal pathogens *P. gaeumannii* and *R. pseudotsugae* was already established during the first examination of health status (Georgieva, 2009) and the defoliation process progresses with the increase of age. It is noteworthy that for some of the continental provenances

Table 3. Growth characteristics of 30 Douglas-fir provenances at the Training and Experimental Forest Range Petrohan

Provenance group	Provenance number	Seed zone	Provenance name	DBH (cm) 2011	DBH (cm) 2020	Zd (cm) 2011	Zd (cm) 2020	H (m) 2011	H (m) 2020	Zh (m) 2011	Zh (m) 2020
			Continental								
New Mexico	55	840	Alamogordo	8.3	12.1	0.3	0.4	6.2	9.8	0.3	0.3
Washington	1	612	Greenwood	12.6	21.6	0.5	0.7	9.9	13.5	0.4	0.4
	2	600	Keremeos	11.8	15.7	0.5	0.5	9.7	13.4	0.4	0.4
East Cascade	16	661	Parkdale	18.2	25.8	0.8	0.8	15.3	21.3	0.6	0.6
Mountains	17	661	Parkdale	18.5	26.7	0.8	0.8	16.1	21.5	0.7	0.7
Oregon	18	661	Parkdale	17.7	27.3	0.7	0.8	16.2	20.5	0.7	0.6
	33	662	Warm Springs	16.1	23.1	0.7	0.7	12.9	20.7	0.5	0.6
	32	662	Warm Springs	16.0	23.8	0.7	0.7	14.9	20.0	0.6	0.6
	47	681	Crescent	18.7	28.3	0.8	0.9	15.7	18.0	0.7	0.5
	48	681	Crescent	16.1	24.3	0.7	0.7	14.7	18.2	0.6	0.6
East Oregon	36	892	Canyon City	12.8	14.8	0.5	0.4	10.4	9.9	0.4	0.3
South Oregon	49	501	Crater Lake	17.9	25.1	0.7	0.8	15.3	20.4	0.6	0.6
	50	501	Medford	17.7	24.6	0.7	0.7	14.9	18.8	0.6	0.6
	51	502	Medford	18	24.3	0.8	0.7	15.2	19.3	0.6	0.6
			Western Cascade Mountains								
Washington	9	411	Monroe	17.4	24.6	0.7	0.7	17.9	19.8	0.7	0.6
	24	452	Idanha	18.2	23.9	0.8	0.7	12.3	21.5	0.5	0.7
	25	452	Idanha	14.5	21.3	0.6	0.6	11.7	20.7	0.5	0.6
	26	452	Idanha	16.7	23.8	0.7	0.7	14.2	20.0	0.6	0.6
	30	452	Idanha	18.4	27.6	0.8	0.8	16.0	20.0	0.7	0.6
	40	472	Oakridge	16.4	21.8	0.7	0.7	13.9	16.2	0.6	0.5
Oregon	41	472	Oakridge	16.6	25.9	0.7	0.8	14.6	20.3	0.6	0.6
	46	472	Oakridge	15.8	24.8	0.7	0.8	12.7	19.0	0.5	0.6
	39	473	Santiam Pass	14.9	25.8	0.6	0.8	11.4	19.0	0.5	0.6
	42	473	Oakridge	17.5	25.2	0.7	0.8	14.8	19.5	0.6	0.6
	43	482	Oakridge	17.4	27.5	0.7	0.8	14.5	16.9	0.6	0.5
			Coast								
Washington	10	222	Bremerton	17.8	26.7	0.7	0.8	16.2	18.1	0.7	0.5
Oregon	34	53	Toledo	15.5	23.2	0.6	0.7	11.5	20.2	0.5	0.6
	52	82	Brookings	19.3	26.2	0.8	0.8	14.6	20.2	0.6	0.6
	53	82	Brookings	19.9	29.3	0.8	0.9	15.9	21.4	0.7	0.6

DBH – average diameter at breast height; Zd – average diameter increment; H – average height; Zh – average height increment.

(55 Alamogordo, 1 Greenwood, 18 Parkdale, 47 Crescent and 49 Crater Lake) a slight increase in diameter increment is observed. This is due to an increase in the growth space, as a result of the death and subsequent felling of a considerable part of the individuals. The larger growth space has stimulated diameter growth. For example, at provenance 55 Alamogordo, only 4 individuals remained alive out of 40 planted; at provenances 1 Greenwood and 47 Crescent – 11 from 48 resp. 46 planted individuals. Decline or retention of height increment was found in half of the provenances from the Western Cascade Mountains, indicating that they were also affected to some increase of degree in defoliation rate. In the rest of the provenances of this group, a slight increase in diameter increment is observed. There are also two provenances (46 Oakridge and 39 Santiam Pass) with an increase in both height- and diameter increments. A similar conclusion we can draw about the Coastal provenances (Table 3).

Data on changes in average height and diameter increment indicate that there is likely to be a relationship between the average current annual increment in these indicators and the defoliation rate. In search of a relationship between growth indicators and the degree of defoliation, regression models were developed.

Relationships between the average current annual height increment by provenance groups for the period 2003–2011 and 2011–2020 were calculated (Fig. 1). Two regression models were presented for the relationship between height increment and defoliation rate for 14 continental provenances. For the period 2003–2011, a high statistical significance at $p < 0.0001$ and a negative coefficient were observed, i.e. the height increment decreases with an increase in the percentage of defoliation (Model A). Similar is model B for the period 2011–2020. It also has a negative coefficient and is statistically significant at $p < 0.05$. The nature of the curve is analogous to that of the previous period.

Similar relationships were obtained between diameter increment and defoliation percentage for all provenance groups and are presented in the following sequence.

Graphical relationships between the average current annual diameter increment and the percentage of defoliation for the four coastal provenances (A for the period 2003–2011 and B – for the period 2011–2020) were presented (Fig. 2). Both models have a high degree of significance ($p < 0.0001$). The dependence is inversely proportional, i.e. diameter increment decreases with increasing defoliation rate.

Similar were the dependencies between the average current annual diameter increment and the percentage of defoliation for the 12 provenances from the Western Cascade Mountains – A for the period 2003–2011 and B – for the period 2011–2020 (Fig. 3). Both models were highly significant at $p < 0.0001$. Here too, with an increase in the percentage of defoliation, the diameter increment decreased.

Models for dependence between the average current annual diameter increment and the percentage of defoliation of the 14 continental provenances – A for the period 2003–2011 and B – for the period 2011–2020 was presented in Fig. 4. Both models had a high degree of significance at $p < 0.0001$. It was established that with an increase in the percentage of defoliation, the diameter increment has decreased.

Rhabdocline needle cast caused by the fungal pathogen *R. pseudotsugae* and Swiss needle cast caused by *P. gaeumannii* were reported on the trees of continental provenances planted in Sofia, SFE Kostenets, Kyustendil and TEFR Petrohan (Georgieva, 2009). Distinct differences among provenances comparing the degree of their susceptibility to both fungal pathogens were observed. A necrotic disease caused by the fungal pathogen *Allantophomopsiella pseudotsugae* (Wilson) Crous was established in 2010 on 20% of trees from sixteen provenances planted in Sofia (Georgieva, 2015). The pathogen caused necrotic formation on the stems of all infected trees, regardless of the geographical origin of the seeds. Development of canker was found on the frost-prone or mechanically damaged sites on stems. The growth within living tissue and height gain were limited. Wilting of branches and death of whole trees were observed.

In this current study, among all provenance groups (continental, coastal, and Cascade Mountains) an inverse linear relationship was found between average current diameter increment and defoliation rate, both in the period after the initial diagnosis of diseases caused by *P. gaeumannii* and *R. pseudotsugae* (2003–2011) and in the period 2011–2020. Similar results were obtained by Osman and Sharrow (1993) for a three-year Douglas-fir plantation. The authors did not report an effect of defoliation on height growth ($p > 0.05$) and observed more losses from defoliation in spring than in summer ($p < 0.05$). No effect of defoliation on seedling survival was found. Reductions in height and basal area of 10– to 30-year-old Douglas-fir stands along the coast of Oregon (USA), due to defoliation caused by *P. gaeumannii*, were reported by Maguire et al. (2011).

In 2011, needle casts diseases caused by *R. pseudotsugae* and *P. gaeumannii* appeared to be the most serious factors limiting the growth of the continental Douglas-fir trees at 24 years of age (Petkova et al., 2014). The results indicated that the coastal provenances from Oregon and Washington demonstrate faster growth than the continental provenances in the local conditions at Training and Experimental Forest Range Petrohan. Among the worst-rated, with no exceptions, were provenances from the interior such as Keremeos (Washington), Whitefish (Montana), Bates (Oregon), and Canyon City (East Oregon) that showed symptoms typical of needle cast together with decreased vitality. In 2020, the results of evaluating the health status in the trial at 24 years of age showed that a serious degree of defoliation was found among all continental provenances. The extent of damage, expressed as the amount of Douglas-fir needles cast, varied among provenance groups.

An inversely proportional relationship between defoliation caused by both pathogens *R. pseudotsugae* and *P. gaeumannii*, and diameter gain was also observed in Poland in 2011 and 2016, comparing the health status of 24 Douglas-fir provenances from the original areal of dis-

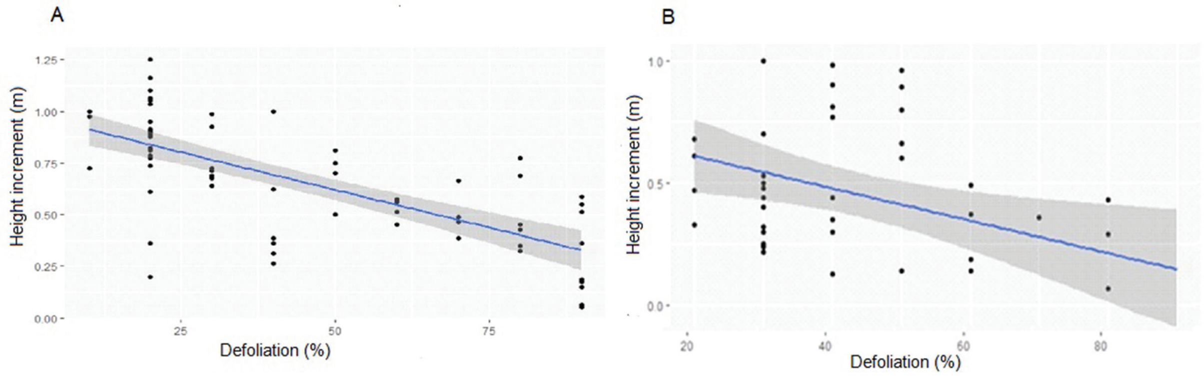

Fig. 1. Dependence between the average current annual height increment and the percentage of defoliation for the group of continental provenances in the period: 2003–2011 (A), 2011–2020 (B).

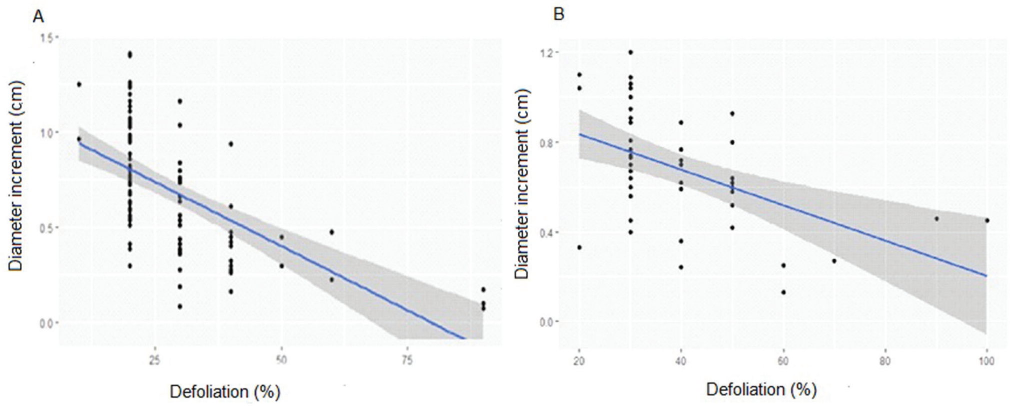

Fig. 2. Relationship between the average current annual diameter increment and the percentage of defoliation for 4 coastal provenances in the period: 2003–2011 (A), 2011–2020 (B).

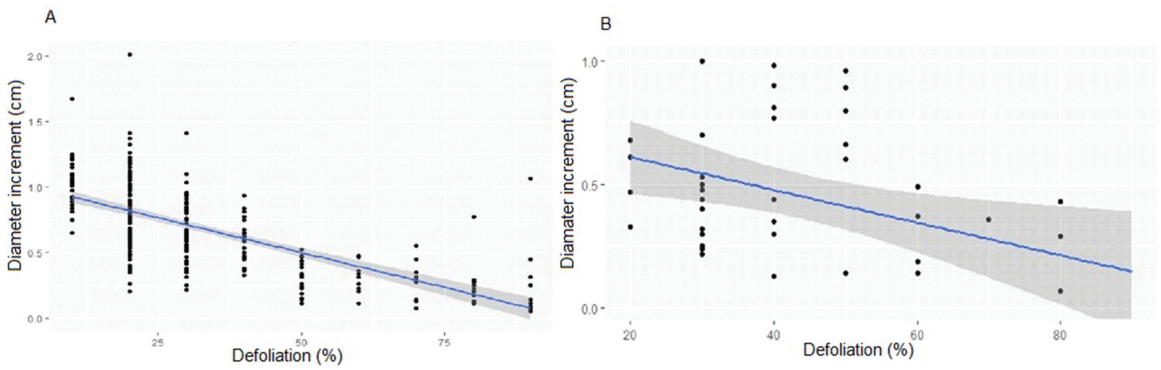

Fig. 3. Relationship between average current annual diameter increment and percentage of defoliation for 12 Western Cascade Mountain provenances in the period: 2003–2011 (A), 2011–2020 (B).

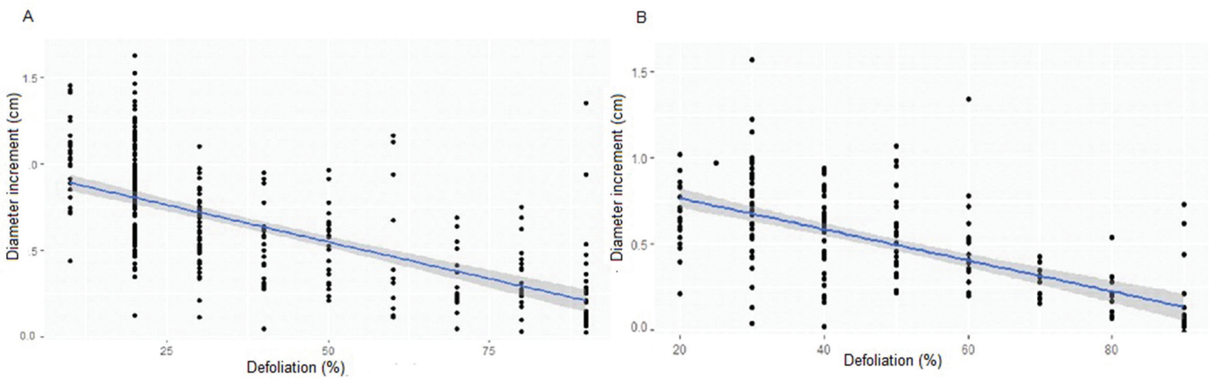

Fig. 4. Relationship between the average current annual diameter increment and the percentage of defoliation for 14 continental provenances in the period: 2003–2011 (A), 2011–2020 (B).

tribution (British Columbia, Washington, Oregon) (Samek et al., 2019). All Washington provenances have maintained satisfactory gains since the previous measurement in 2011, and were almost not affected at all by pathogens from the *Rhabdocline* and *Phaeocryptopus* genera. According to their observations, some provenances from British Columbia and Oregon are not suitable for plantation under Central European conditions, because of the high defoliation rate.

Kurkela (1981) found a clear negative correlation between height increment and defoliation rate due to *R. pseudotsugae* and *P. gaeumannii*. Radial growth is also affected by disease, but to a lesser extent than height. In our study, a negative correlation was found between height increment and defoliation rate for continental provenances (Fig. 1). As a consequence of the disease caused by the fungal pathogen *P. gaeumannii*, the growth in height and diameter, as well as the total volume of Douglas-fir is reduced (Hansen et al., 2000; Maguire et al. 2002; Mańka, 2005; Łakomy and Iwańczuk, 2010). The reduction correlated significantly with the degree of defoliation. Persistent and severe infections of younger (10–30 years old) and older (80 years old) Douglas-fir stands can reduce growth by 52% (Maguire et al. 2002) and diameter growth by up to 85% (Black et al., 2010). A reduction in the growth of Douglas-fir plantations in New Zealand due to the same pathogen was also reported by Watt et al. (2010) and Kimberley et al. (2011); a reduction in height growth by 25%, in basal area by 27% and in volume by 32% was also reported for New Zealand.

The most significant disease impacting on the vigor of Douglas-fir is caused by *R. pseudotsugae*. This pathogen is specific to Douglas-fir, and was probably introduced into Europe in the early 20th century. The disease can cause massive reductions in vigor to Douglas-fir plantations in the Pacific North West, where the pathogen and host are native, but rarely results in significant losses in native forests.

In Europe, particular varieties of Douglas-fir vary in response to *R. pseudotsugae*, with *P. menziesii* var. *viridis* being more commonly planted than the caesia and glauca variety, due to lower susceptibility (Bednářová et al., 2013). Severe losses of current year needles can occur when conditions are conducive to infection; such conditions include high humidity conditions in the spring.

With regression models, an inversely proportional relationship between the degree of defoliation and the height increment of the continental provenances was established, i.e. as the degree of defoliation increases, the increment decreases. A similar relationship was found between the degree of defoliation and diameter increment for all provenance groups.

The most suitable provenances with rapid growth, highest productivity and resistance to needle cast diseases were Parkdale (Oregon, continental areas), Oakridge and Santiam Pass (Oregon, Western Cascade Range), Bremerton (Washington, Western Cascade Range), and Toledo, Brookings and Brookings (Oregon, East Coast).

Conclusions

The results of the conducted surveys in 2011 and 2020 showed that there were significant differences between the individual Douglas-fir provenances in relation to their susceptibility to the needle cast diseases, caused by the fungal pathogens *R. pseudotsugae* and *P. gaeumannii*. The extent of defoliation varied among provenance groups in individual years. A serious degree of defoliation was found among the continental provenances Alamogordo (New Mexico), Greenwood and Keremeos (Washington), and Canyon City (Eastern Oregon). The loss of needles and the reduced physiological function of the trees affected their vitality in the following years.

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