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Dendrochronological data from twelve countries proved definite growth response of black alder (*Alnus glutinosa* [L.] Gaertn.) to climate courses across its distribution range

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Abstract

Black alder (*Alnus glutinosa* [L.] Gaertn.) is an important component of riparian and wetland ecosystems in Europe. However, data on the growth of this significant broadleaved tree species is very limited. Presently, black alder currently suffers from the pathogen *Phytophthora* and is particularly threatened by climate change. The objective of this study was to focus on the impact of climatic variables (precipitation, temperature, extreme climatic events) on the radial growth of alder across its geographic range during the period 1975–2015. The study of alder stands aged 46–108 years was conducted on 24 research plots in a wide altitude range (85–1015 m) in 12 countries of Europe and Asia. The most significant months affecting alder radial growth were February and March, where air temperatures are more significant than precipitation. Heavy frost and extreme weather fluctuations in the first quarter of the year were the main limiting factors for diameter increment. Within the geographical setting, latitude had a higher effect on radial growth compared to longitude. However, the most important variable concerning growth parameters was altitude. The temperature's effect on the increment was negative in the lowlands and yet turned to positive with increasing altitude. Moreover, growth sensitivity to precipitation significantly decreased with the increasing age of alder stands. In conclusion, the growth variability of alder and the number of negative pointer years increased with time, which was caused by the ongoing climate change and also a possible drop in the groundwater level. Riparian alder stands well supplied with water are better adapted to climatic extremes compared to plateau and marshy sites.

Key words: riparian and wetland ecosystems; tree ring width; diameter increment; precipitation; air temperature

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1. Introduction

Black alder (*Alnus glutinosa* [L.] Gaertn.) is a pioneer tree species with a wide range of distribution (Claessens et al. 2010; Socha & Ochał 2017). The primary habitats of this tree species are alluvial forests and other wet to muddy areas (Natlandsmyr & Hjelle 2016), especially waterlogged marshy and riparian sites (Kamocki et al. 2018). Alder can grow in regularly flooded areas (Glenz et al. 2006; Elferts et al. 2011), as one of its key ecological characteristics is accommodation to high groundwater

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levels by an adaptable root system and high transpiration potential (Ellenberg et al. 1992; Brus 2005; Laganis et al. 2008; Elferts et al. 2011). It occurs naturally from central Scandinavia in the north, across Europe, to North Africa in the south (Kajba & Gracan 2003). Its range extends from the western Iberian Peninsula in the west to the mountainous regions of Turkey in the east (King & Ferris 1998; Rodrígues-González et al. 2004, 2008).

Black alder is a typical yet scattered component (< 1%) of mixed deciduous forest in its range (Turok et al. 1996). This broadleaf has a higher abundance (≤ 5%) in northern European countries (Claessens et al. 2010; Kamocki et al. 2018) and in south-central Europe, where it often forms vast, highly productive stands (Socha & Ochał 2017). Black alder has a good timber production potential (Claessens et al. 2002; Salca 2019). Mesic habitats are yet a key prerequisite for extensive production of high-quality alder timber in its ecological optimum (Eschenbach & Kappen 1999; Claessens et al. 2010).

From an ecological perspective, alder plays a crucial role in ecosystem processes and nitrogen fixation (Vogel et al. 1997; Roy et al. 2007; Aosaar et al. 2013; Uri et al. 2014), which is facilitated by symbiotic bacteria of the genus *Frankia* on the roots (Oliveira et al. 2005; Hytönen & Saarsalmi 2015). This tree species also contributes considerable biodiversity greatl by providing habitats for specific fauna and flora (Dussart 1999; Kamocki et al. 2018). On the other hand, *Alnus* may pose a threat to the current species composition in water-influenced habitats with high conservation value (Natlandsmyr & Hjelle 2016) due to the aforementioned nitrogen enrichment (Vogel et al. 1997; Mander et al. 2008; Kamocki et al. 2018). Its high tolerance to unfavorable climatic and ecological conditions, where other tree species' growth is limited (Tobita et al. 2010; Vacek et al. 2016), enables this plastic species to help reclaim disturbed soils (Roy et al. 2007; Krzaklewski et al. 2012; Vacek et al. 2018). Alder also improves water filtration and purification in waterlogged soil (Schnitzler & Carbiener 1993), and their root systems partially restrict floods by stabilizing river banks (Piégay et al. 2003; Rodrígues-González et al. 2014).

However, in the context of ongoing global climate change, these riparian and wetland habitats are strongly threatened by changes in precipitation distribution, temperature, and runoff patterns (Palmer et al. 2009), which are closely related to the loss of alder stands (Tulik et al. 2020; Valor et al. 2020). Alder dieback due to climate change is also additionally compounded by the pathogen *Phytophthora* (Malewski et al. 2020; Nave et. al. 2021). A reliable indicator of these environmental changes may be the radial tree growth influenced by complex environmental variables occurring at a given site (Whitehead 1998). Radial tree growth responds very dynamically to the current combination of environmental conditions (Waring 1987; Laganis et al. 2008). Thus, the radial ring width can be used to monitor a range of environmental factors, such as climate and weather extremes, soil fertility, insect gradation, or competition (D'Arrigo et al. 2008; Rodrígues-González et al. 2010; Vacek et al. 2021a). In the case of tree species growing in wet habitats, water availability is vital as a major factor limiting tree growth (Elferts et al. 2011). With this knowledge, it is possible to use radial increment as an indicator of the functioning of wetland forest ecosystems in different years and to reconstruct preceding water levels (Lara et al. 2005; Laganis et al. 2008). Therefore, records of historical values of climate parameters in relation to radial tree growth are very important, both for understanding the evolution of climate and for the subsequent optimization of management measures in particular forest ecosystems (Palmer et al. 2008; Rodrígues-González et al. 2014). This comprehensive work will contribute to a more detailed understanding of the long-term growth dynamics of alder stands, which have so far received only marginal and local attention compared to other tree species (Elferts et al. 2011; Vacek et al. 2016). The study aimed to assess the influence of climate on the radial growth of black alder in different Eurasian habitats, namely from England to Italy and east-westwards from Spain to Turkey. Specific objectives were to determine (i) the dynamics of alder radial growth under the ongoing global climate change, (ii) the effect of mean monthly air temperature and precipitation on alder radial growth, and (iii) the effect of geographic location (latitude, longitude, altitude) and associated climate (oceanic to continental) on radial growth of riparian and wetland alder stands.

2. Material and Methods

2.1. Study area

The research is conducted on 24 research plots in the following 12 countries in Europe and Asia: Great Britain (GBR 2×), Spain (ESP 2×), Slovakia (SVK 2×), Germany (DEU 1×), Italy (ITA 1×), Czechia (CZE 4×), Austria (AUT 1×), Poland (POL 4×), Lithuania (LTU 1×), Belarus (BLR 1×), Ukraine (UKR 1×), and Turkey (TUR 4×; Fig. 1). The study areas are bounded by latitude 54°16'42"N in the north, latitude 40°36'41"N in the south, longitude 31°27'22"E in the east, and longitude 3°13'29"W in the west. The altitude range of the research plots is from 85 to 1015 m a.s.l. with the and the slope variance in the range of 0–17°. The climate is very diverse and is classified according to the Köppen climate classification system (Köppen 1936). The areas of interest belong to the following four regions: Cfb (temperate oceanic climate), Dfb (war –summer humid continental climate), Dfc (subarctic climate), Csb (war –summer Mediterranean climate). The mean annual temperature falls in the range of 4.6–14.8 °C, and the total annual precipitation ranges from 540 to 1405 mm. The mean vegetation period (the longest continuous period of non-freezing temperatures) lasts from 135 to 320 days. An

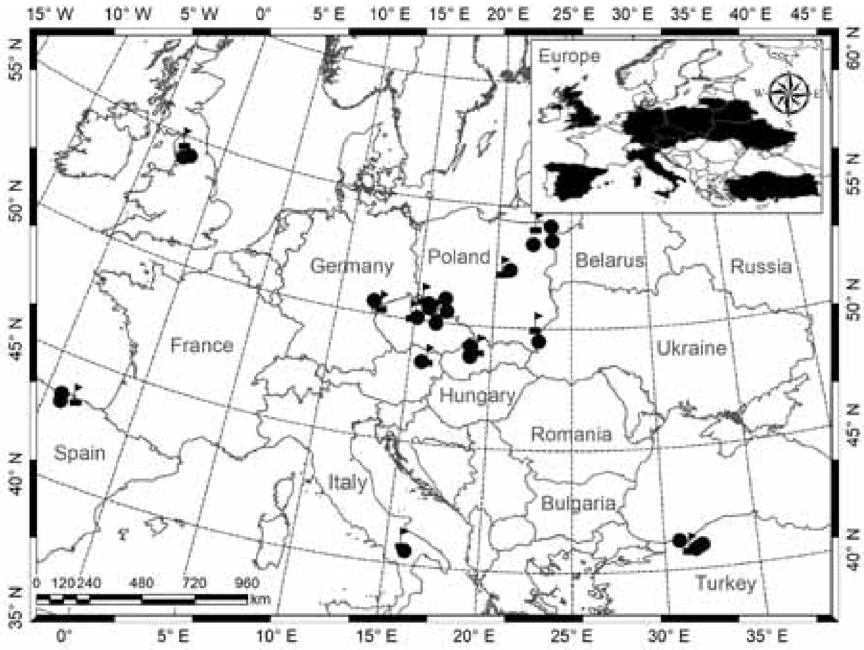

Fig. 1. Location of 24 research plots (•) with black alder forest stands in 12 countries in Europe and Asia, and 13 meteorological stations (⚑) used for dendrochronology analyses.

Table 1. Overview of the basic characteristics of alder research plots (left) and meteorological stations used for tree-ring dating (right).

Plot ID	Age	WGS84		State	Altitude	Climate	Meteorol.	WGS84		Altitude
	[yr]	NS	EW		[m a.s.l.]	class.*	station	NS	EW	[m a.s.l.]
GBR 195	103	54°15’46”N	2°55’55”W	Britain	195	Cfb	Ambleside	54°25’48”N	2°57’36”W	100
GBR 230	108	54°16’42”N	2°55’40”W	Britain	230	Cfb	Ambleside	54°25’48”N	2°57’36”W	100
ESP 260	77	43°19’28”N	3°13’29”W	Spain	260	Cfb	Bilbao	43°15’36”N	2°55’48”W	35
ESP 530	47	43°18’21”N	3°13’12”W	Spain	530	Cfb	Bilbao	43°15’36”N	2°55’48”W	35
ITA 715	55	40°36’41”N	15°47’42”E	Italy	715	Csb	Abriola	40°30’28”N	15°48’47”E	1050
DEU 590	96	50°21’36”N	12°27’45”E	Germany	590	Dfb	Karlovy Vary	50°12’6”N	12°54’52”E	600
CZE 325	52	50°0’36”N	14°51’34”E	Czechia	325	Cfb	Ondřejov	49°54’24”N	14°47’6”E	485
CZE 645	68	50°15’34”N	16°20’55”E	Czechia	645	Dfb	Deštné v OH	50°18’1’’N	16°21’51’’E	650
CZE 780	68	50°42’9”N	15°49’49”E	Czechia	780	Dfc	Pec pod Sněž.	50°41’30’’N	15°43’43’’E	815
CZE 895	66	50°42’36”N	15°50’13”E	Czechia	895	Dfc	Pec pod Sněž.	50°41’30’’N	15°43’43’’E	815
AUT 275	77	48°11’29”N	16°13’55”E	Austria	275	Cfb	Viennna	48°7’1”N	16°34’1”E	180
POL 85	86	52°21’33”N	21°5’10”E	Poland	85	Dfb	Warsaw	52°9’43”N	21°1’49”E	100
POL 125	63	53°43’28”N	22°30’19”E	Poland	125	Dfb	Suwałki	54°6’36”N	22°55’48”E	180
POL 535	82	50°23’52”N	16°25’9”E	Poland	535	Dfb	Deštné v OH	50°18’1’’N	16°21’51’’E	650
POL 755	48	50°28’55”N	16°21’13”E	Poland	755	Dfb	Deštné v OH	50°18’1’’N	16°21’51’’E	650
LTU 130	47	54°10’36”N	23°26’41”E	Lithuania	130	Dfb	Suwałki	54°6’36”N	22°55’48”E	180
BLR 115	60	53°51’29”N	23°32’2”E	Belarus	115	Dfb	Suwałki	54°6’36”N	22°55’48”E	180
UKR 690	87	49°20’2”N	22°44’38”E	Ukraine	690	Dfb	Przemyśl	49°47’24”N	22°46’12”E	195
SVK 290	71	48°34’41”N	19°0’9”E	Slovakia	290	Dfb	Sliač	48°38’8”N	19°8’15”E	320
SVK 310	57	48°34’53”N	19°0’17”E	Slovakia	310	Dfb	Sliač	48°38’8”N	19°8’15”E	320
TUR 205	49	40°54’55”N	31°12’7”E	Turkey	205	Cfb	Bolu	40°44’24”N	31°36’36”E	730
TUR 395	46	40°52’1”N	31°18’10”E	Turkey	395	Cfb	Bolu	40°44’24”N	31°36’36”E	730
TUR 680	60	40°53’6”N	31°19’59”E	Turkey	680	Cfb	Bolu	40°44’24”N	31°36’36”E	730
TUR 1015	48	40°46’13”N	31°27’22”E	Turkey	1015	Dfb	Bolu	40°44’24”N	31°36’36”E	730

Notes: *climate classified according to the Köppen classification system (Köppen 1936).

overview of the basic information on the research plots and the used meteorological station is in Table 1.

The study stands dominated by black alder belonged to the associations *Alnion incanae* Pawłowski et al. 1928, *Alnenion glutinoso-incanae* Oberdorfer 1953, *Stellario nemorum-Alnetum glutinosae* Lohmeyer 1957, *Arunco sylvestris-Alnetum glutinosae* Tuxen 1957, *Carici remotae-Fraxinetum excelsioris* Koch ex Faber 1936, and *Piceo abietis-Alnetum glutinosae* Mraz 1959. Other admixed tree species occurring in the tree layer included predominately Norway spruce (*Picea abies* [L.] Karst.), grey alder (*Alnus incana* [L.] Moench), European ash (*Fraxinus excelsior* L.), sycamore maple (*Acer pseudoplatanus* L.), goat willow (*Salix caprea* L.), silver birch (*Betula pendula* Roth.), Scots pine (*Pinus sylvestris* L.), European beech (*Fagus sylvatica* L.), eastern beech (*Fagus orientalis* Lipsky), oriental plane (*Platanus orientalis* L.), Sitka spruce (*Picea sitchensis* [Bong.] Carr.) and oaks (*Quercus* sp.). From the pedological point of view, the predominant soil types are Gleysols, Fluvisols, Stagnosols, and gleyic Cambisols (WRB 2014). The bedrock is formed by a wide range of rock, from alluvial clays and gravels, through phyllites and shales to granitoids. The age of the studied alder stands was in the range of 46–108 years.

2.2. Data collection

For the analysis of radial growth, core samples were obtained from the alder trees with a Pressler auger (Haglöf, Sweden) at a height of 1.3 m in the direction up/down the slope. From each research plot, 20 samples from the co-dominant and dominant live trees according to the Kraft classification (Kraft 1884) were randomly (RNG function, Excel) selected as the significant growth response (compared to subdominant and suppressed trees; Remeš et al. 2015). In the plots with a limited number of suitable alder trees (social status, no rot, straight trunk, no break, etc.), at least 12 core samples were obtained for dendrochronological analyses. A total of 381 core samples of alder trees were collected (358 samples analyzed). The annual increments of tree rings were then measured with an accuracy of 0.01 mm using an Olympus binocular microscope on a LINTAB measuring table and recorded in TsapWin software (Rinntech).

Measurements from meteorological stations were used to derive the effect of climate and stress factors on radial growth. Available data from the Ambleside station for Great Britain, Bilbao station for Spain, Sliač station for Slovakia, Karlovy Vary station for Germany, Abriola station for Italy, Deštné v Orlických horách, Pec pod Sněžkou, and Ondřejov stations for Czechia, Vienna for Austria, Deštné v Orlických horách, Warsaw, and Suwałki stations for Poland, Suwałki station for Lithuania and Belarus, Przemyśl station for Ukraine, and Bolu station for Turkey were used for the analysis of the temperature and precipitation conditions in the period of 1975–2015. The distance between the meteorological stations and research plots was in the range of 5–46 km. The development of temperature and precipitation conditions was based on the data of the temperature in individual months, the average annual temperature, the temperature in the vegetation period, annual total precipitation, total precipitation in the vegetation period, total monthly precipitation, and extreme climatic events.

2.3. Data analysis

Tree-ring increment series of alder were individually cross-dated to remove errors caused by missing tree rings using statistical tests in the PAST application (Knibbe 2007). These series were subsequently subjected to a visual inspection according to Yamaguchi (1991). If a missing tree ring was revealed, a tree ring of 0.01 mm in width was inserted in its place. Individual curves from research plots were detrended, and an average tree-ring series was created in the ARSTAN program (Tree Ring Laboratory, USA). Negative exponential spline and subsequently, 0.67n spline was used for age detrending (Grissino-Mayer et al. 1992).

The analysis of negative pointer years (NPY) was accomplished by Schweingruber (1990) and Desplanque et al. (1999). For each tree, a pointer year was identified as an extremely narrow tree ring that does not reach 40% of the increment average from the four preceding years. The occurrence of the negative year was proved if a strong reduction in increment occurred in at least 20% of trees on the plot. To express the relationship between climate characteristics (monthly average air temperatures and sum of precipitation in particular years) and radial growth, the DendroClim software was used (Biondi & Waikul 2004).

Principal component analysis (PCA) was performed using the CANOCO 5 program (Microcomputer Power, USA) to evaluate the relationships between the radial growth variability, growth sensitivity to climate factors (temperature, precipitation), stand age, altitude, latitude, longitude, and research plots. Before the analysis, the data was standardized and centralized. The results of PCA were illustrated by an ordination diagram. Pearson correlations were performed in Statistica 12 software (Statsoft, USA) for the evaluations of relationships between climate sensitivity, radial growth variability, tree age, altitude, and geographical position. The map was made in ArcGIS 10 software (Esri, USA).

3. Results

3.1. Dynamics of radial growth

The radial growth of black alder trees showed a different growth dynamic between the individual research areas across Eurasia (Fig. 2). In terms of ring width index (RWI) variability, the highest fluctuations in growth were found in lower-lying areas in Central Europe (CZE 325 – SD 0.257, CZE 645 – SD 0.255, SVK 290 – SD 0.238, and SVK 310 – SD 0.222). On the other hand, low RWI variability was observed in the lowlands of north Poland (POL 85 – SD 0.122, POL 125 – SD 0.133) and the Baltics (LTU 130 – SD 0.133). In terms of NPY characterized by the extremely low diameter increment, the highest number of NPYs (3) were observed in the altitude-highest situated plots in Czechia (CZE – 895) and in the second altitude-highest situated plots from all research plots. In contrast, no NPY was found in the following areas: ESP 530, ITA 715, POL 85, PLO 535, POL 755, LTU 130, TUR 680, and TUR 1015. When dividing the observed period into two halves, a 4× higher number of NPYs (20) were analyzed in the second half of the observed period (1995–2015) compared to the first one (only 5 NPYs). Similarly, the growth variability of ring-width increased with time.

Specifically, NPYs for alder were 1987, 1996, 2010, and 2011 in the mountain areas in Czechia. These years had extremely frosty episodes from January to March. Moreover, the year 1987 was characterized by the historically (since 1975) lowest average temperature in January (−9.5 °C, mean −3.8 °C) and March (−5.5 °C, mean −0.2 °C). The year 1996 had the lowest amount of precipitation/snow in the non-vegetation season (390 mm, mean 686 mm). The NPY 2010 showed the highest variability in monthly temperature during the year, similarly for Germany. In Slovakia, NPYs were 1987 and 2007 for both locations. In 1987, the lowest temperature was observed in March since 1975 (−1.4 °C, mean 3.6 °C). The year 2007 was exceedingly above average in temperature (9.6 °C, mean 8.1 °C), and the temperature in January reached a historical maximum (2.4 °C, mean −3.2 °C), and no precipitation was recorded in April (mean 46 mm). In Austria, NPY 2002 was characterized by the second-highest temperature in February (4.7 °C, mean 0.5 °C), and the year 2003 was the driest period from February to March (3 mm, mean 51 mm). In Turkey, the highest sum of precipitation in February and March (+ 139% above

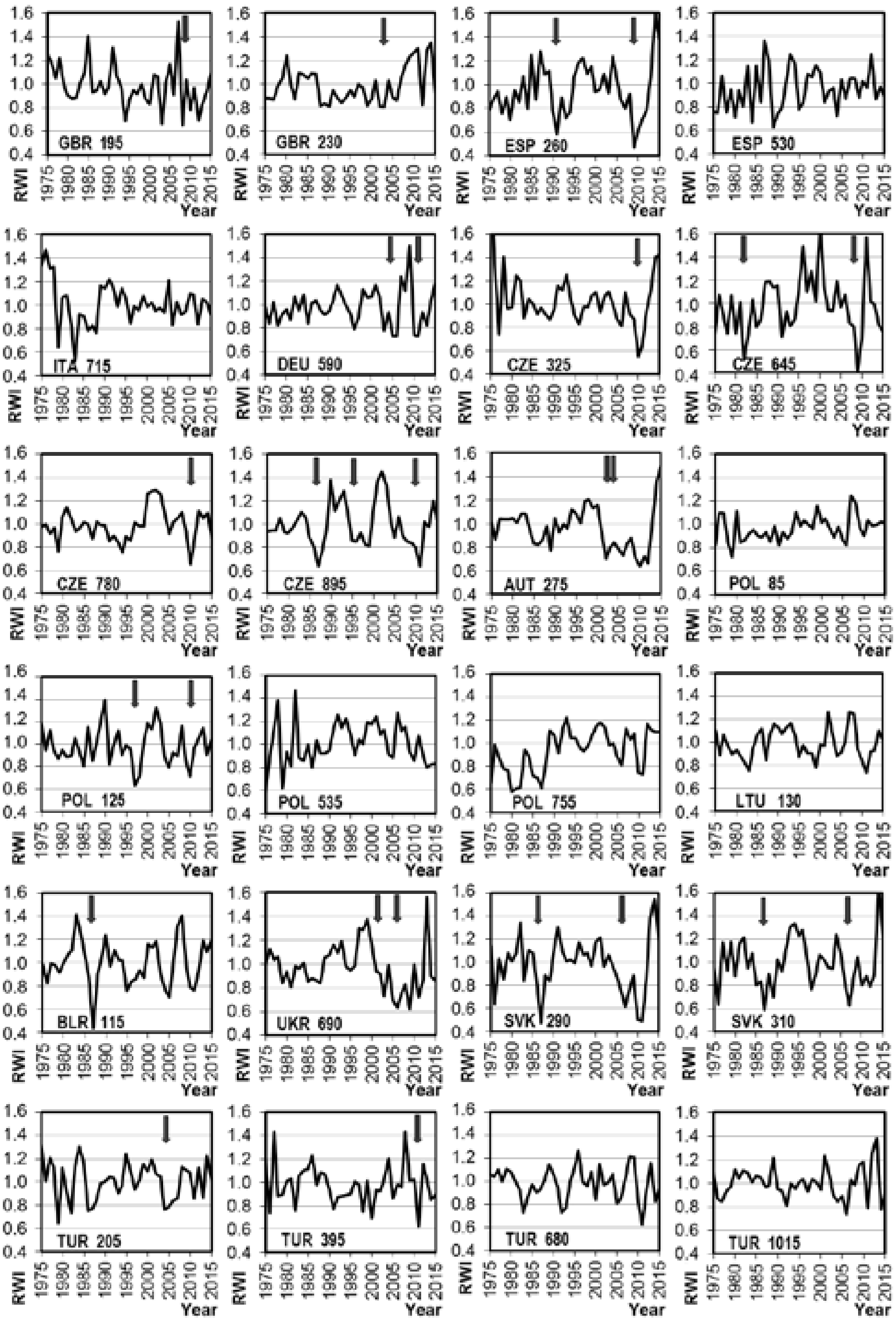

Fig. 2. Standardized mean chronology (ring width index – RWI) of black alder in 1975–2015 after removing the age trend expressed by the tree-ring width index and significant low radial growth expressed by negative pointer years (arrows); the plot code indicates state and altitude (more information in Table 1).

mean) was typical for NPY 2004, and NPY 2011 was characterized by a very cold April (7.5 °C, mean 9.9 °C) and a high temperature variability during the year.

3.2. Effect of air temperature and precipitation

Monthly temperatures significantly ($p < 0.05$) affect the radial growth of alder (Fig. 3). The highest number of significant months was found in mountain areas in Poland (POL 755 – 8 months) and the Czech Republic (CZE 895 – 7 months). Conversely, in the research plots of GBR 315, SVK 290, and TUR 395, no significant ($p > 0.05$) effect of monthly temperatures on alder diameter increment was found. Temperatures had a prevailing significant ($p < 0.05$) positive effect on growth, especially in mountainous areas. The negative effect of temperature was found primarily in the lowlands and warmer regions (e.g., Spain). This trend can be seen in Turkish research

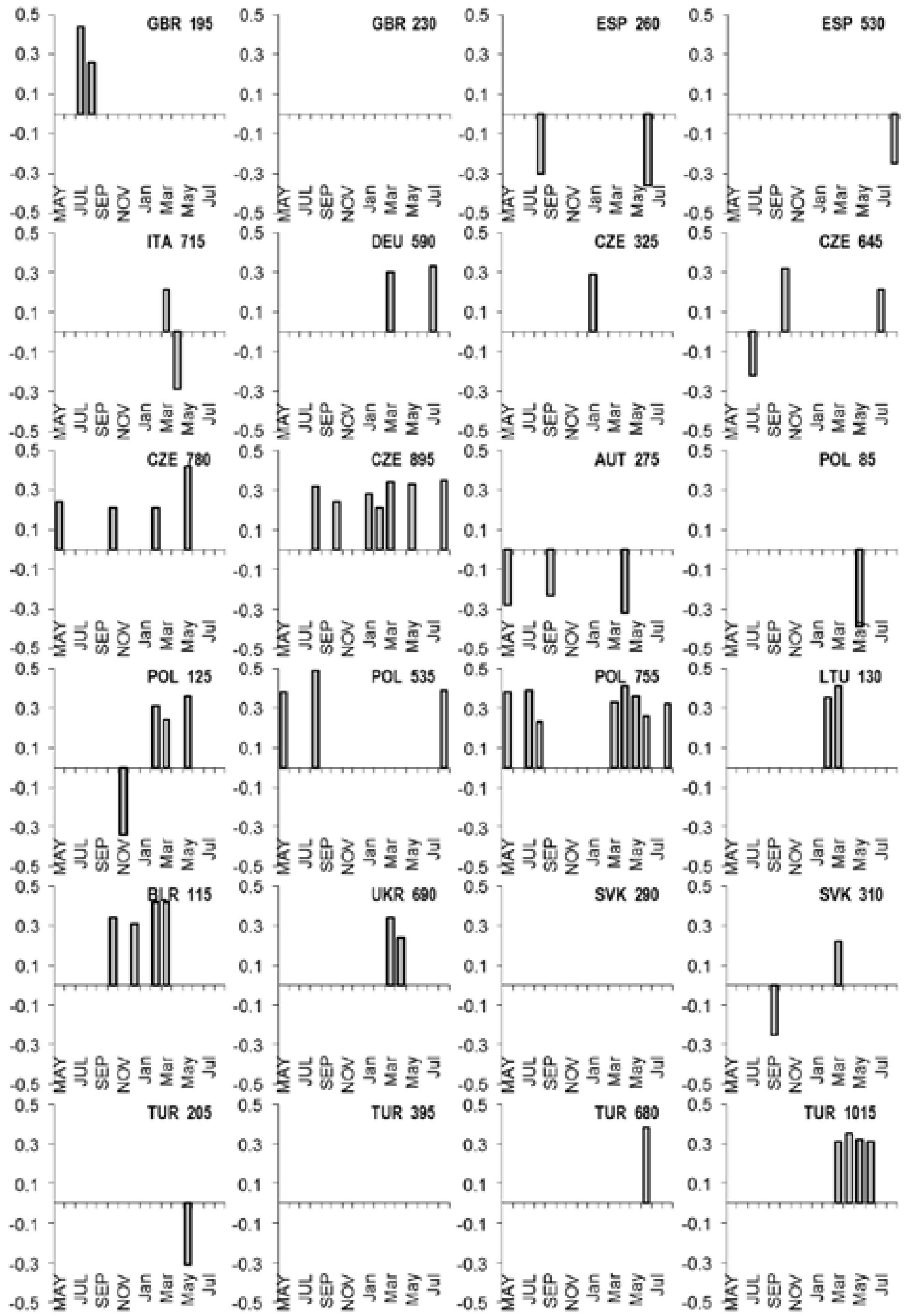

Fig. 3. Coefficients of correlation of the regional residual index tree-ring chronology of black alder with monthly air temperatures from May of the previous year (capital letters) to August of the current year (lower-case letters) in the period 1975–2015; only statistically significant ($p < 0.05$) values are shown; the plot code indicates state and altitude (more information in Table 1).

plots, where 1 significantly ($p < 0.05$) negative month was found in the lowest area (TUR 205), while 4 positive months were found in the highest area (TUR 1015) in terms of the effect of temperatures. Similarly, in Czechia, only 1 correlation was found in the lowlands (CZE 325), 3 correlations in the highlands (CZE 645), and even 7 positive correlations in the mountains (CZE 895). In general, the effect of monthly temperatures in the current year was significantly higher (39 months) compared to the previous year (20 months). Temperatures from February to June had the highest effect on alder radial growth, while the most significant ($p < 0.05$) month (10) was recorded in March.

Precipitation had a significantly lower effect on radial growth compared to temperatures (39 vs. 59 significant months) due to the predominance of waterlogged and

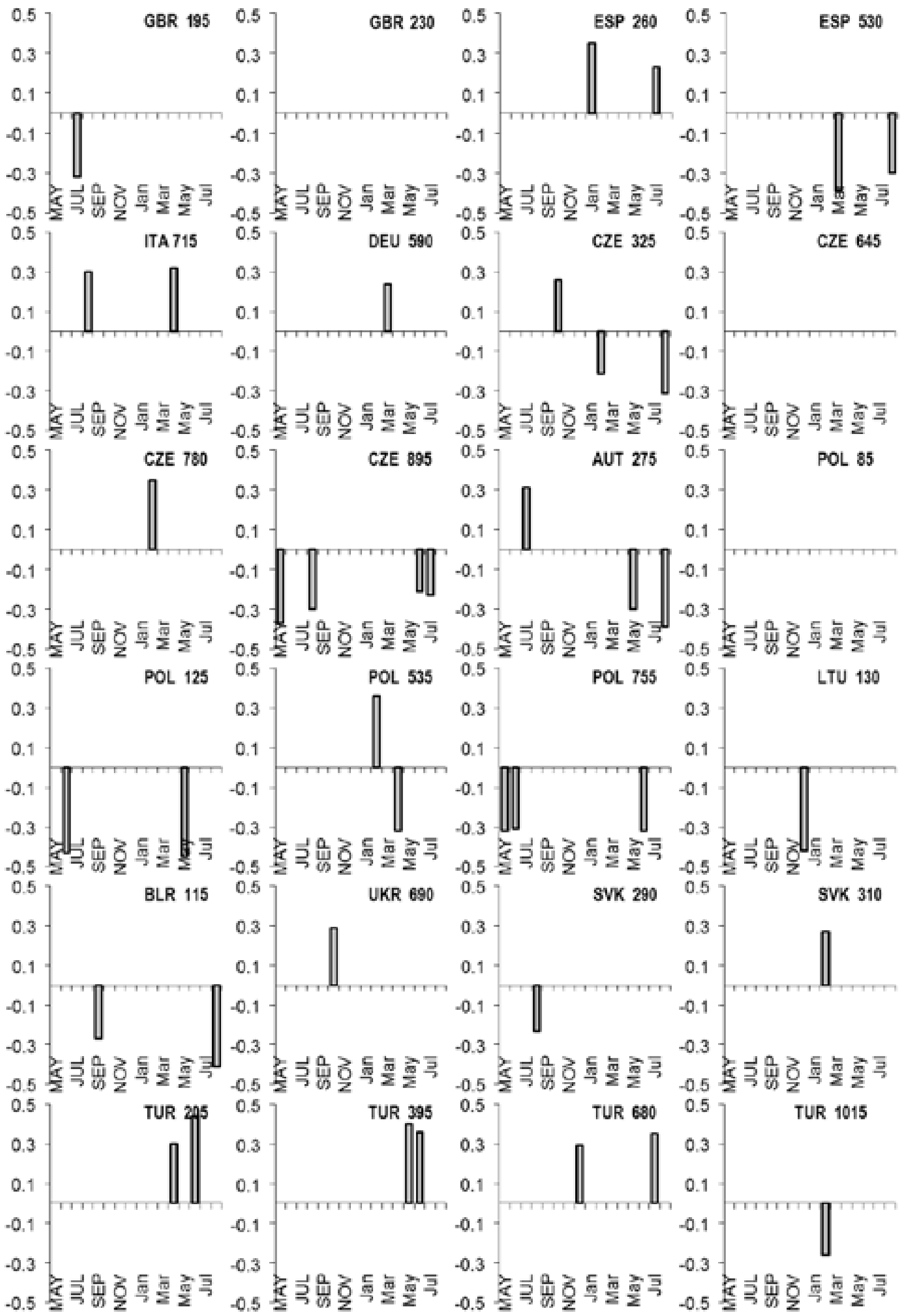

Fig. 4. Coefficients of correlation of the regional residual index tree-ring chronology of black alder with monthly sum of precipitation from May of the previous year (capital letters) to August of the current year (lower-case letters) in the period 1975–2015; only statistically significant ($p < 0.05$) values are shown; the plot code indicates state and altitude (more information in Table 1).

riparian habitats of alder stands (Fig. 4). Precipitation had a predominantly negative significant ($p < 0.05$) effect on diameter increment of alder (22 months negative correlation, 17 months positive correlation). Conversely, when compared with temperatures, precipitation had a positive effect, especially in lowlands and warmer regions (e.g., Italy, Turkey) compared to mountain areas, where the negative effect of precipitation prevailed. The effect of precipitation with increasing altitude changed from positive to negative, which is documented, for example, in research plots in Spain, Turkey, and the Czech Republic. Similar to temperatures, the current year (25 significant months) played a more significant role than the previous year (14 months) in the case of the effect of precipitation on radial growth. Precipitation in February of the current year had the most significant effect on alder growth (5 months), while no effect of precipitation was found in November of the previous year (0 months).

3.3. Interaction between growth and geographical setting

The results of PCA are presented in an ordination diagram showing the relationships among the radial growth variability, negative pointer years, growth sensitivity to temperature and precipitation, tree age, altitude, latitude, longitude, and research plots (Fig. 5). The first ordination axis explains 44.2% of data variability, the first two axes together explain 66.5%, and the first four axes 90.2%. The x–axis illustrates the longitude and age of the tree layer. The y–axis illustrates the altitude of research plots. The growth variability was significantly positively correlated with NPY ($p < 0.05$, $r = 0.41$). Growth sensitivity to temperature (effect of temperature in a particular month) was significantly correlated with altitude ($p < 0.05$, $r = 0.44$) and growth sensitivity to precipitation ($p < 0.05$, $r = 0.42$). Moreover, growth sensitivity to precipitation was significantly decreasing with the increasing age of alder stands ($p < 0.05$, $r = -0.41$). The temperature had a higher explanatory effect in the diagram compared to precipitation. In relation to the geographical setting, latitude was a higher explanatory variable compared to longitude. However, the most important variable concerning growth parameters was the altitude.

4. Discussion

4.1. Dynamics of growth and alder ecology

To understand the function of forest ecosystems and the nature of ecological niches, it is very important to monitor

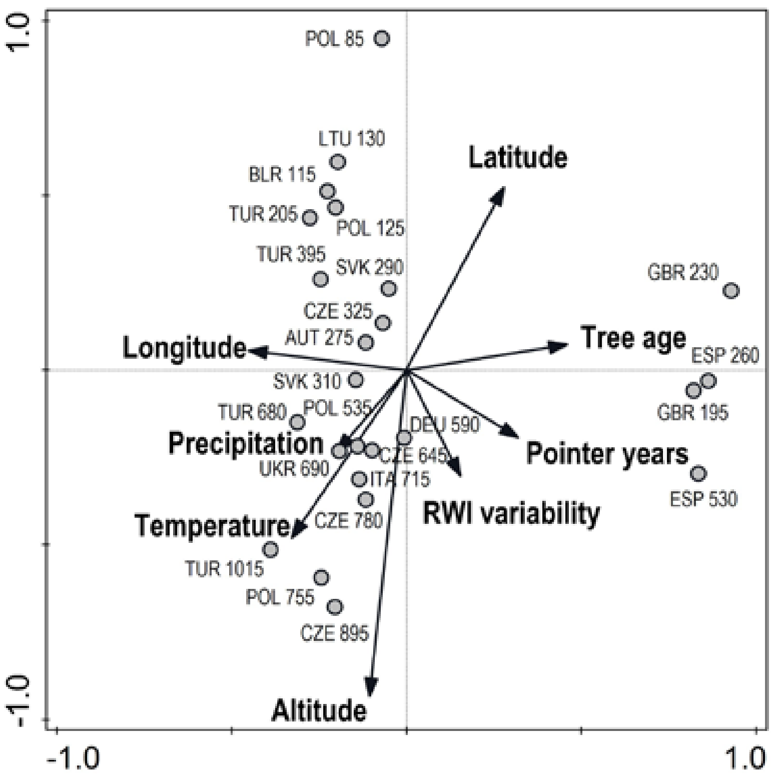

Fig. 5. Ordination diagram showing results of the principal component analysis of relationships between variability of radial width index (RWI), negative pointer years, growth sensitivity to temperature and precipitation (on the base of significant monthly data), tree age, altitude, longitude, and latitude; Symbols • indicate 24 research plots with an abbreviation of state and altitude (more information about the research plots in Table 1 regarding the plot code).

their growth and development, especially under conditions of global climate change (Laganis et al. 2008; Vacek et al. 2017a; Hájek et al. 2020). A substantial characteristic of forest ecosystems is the radial growth of ligneous species, which reflects their annual evolution depending on habitat fertility, stand structure, and climatic conditions (Cukor et al. 2019; Šimůnek et al. 2021; Vacek et al. 2021b). Black alder is an outstanding deciduous tree species with many ecological peculiarities, but with considerable economic importance (Claessens et al. 2002). Alder forests are often among the last remnants of natural wetland and riparian forests of this kind in Central Europe (Nemesszeghy 1986; Jakubisová et al. 2012; Vacek et al. 2016). The decline in the area of these stands is mainly a consequence of the drop in groundwater levels (Levanic & Kotar 1996; Keeland & Sharitz 1997; Pretzell et al. 1997; Slezák et al. 2017). Black alder communities are well-documented from a phytocenological point of view at different geographical scales (Douda 2008; Paal et al. 2007; Slezák et al. 2014; Biurrun et al. 2016). The aforementioned studies suggest that these communities are gradually decreasing in size and experiencing a reduction in radial growth due to global changes.

Similarly, our research, covering 12 countries in Europe and Asia, documented that in recent years there has been an increase in the variability of radial growth in alder stands and an increase in the occurrence of NPYs, which characterize years with extremely low diameter increment. This growth trend over the last 20 years has been confirmed in Central Europe for several other native and introduced tree species (Hájek et al. 2021; Vacek et al. 2021c). As climate change progresses, the number of extreme weather events haves increased, such as long-term droughts, extreme heatwaves, or wind disturbances (Seidl et al. 2014; Šimůnek et al. 2020).

At the same time, it should be emphasized that this study was conducted exclusively in stands dominated by alder. Studies focusing on tree species growing in mixed stands have shown a higher tolerance of individual species to climatic fluctuations (Neuner et al. 2015; Pretzsch et al. 2020a, 2020b). This effect can also be expected in the case of black alder. However, due to the ecological requirements of alder, which is bound to habitats sufficiently supplied with water (Eschenbach & Kappen 1999; Claessens et al. 2010), this tree species' potential for forming mixtures with other genera is limited. An example of suitable mixtures on water-influenced habitats is the combination of black alder with Norway spruce, silver fir (*Abies alba* Mill.), and silver birch in the Southern Carpathians (Dincă et al. 2020) and the other various tree species including oriental spruce (*Picea orientalis* [L.] Link.), oriental beech (*Fagus orientalis* Lipsky), Caucasian fir (*Abies nordmanniana* L. [Steven] Spach), and sweet chestnut (*Castanea sativa* Mill.) in the mesic Black Sea Region of Turkey (Sariyildiz 2015). On our research plots, Norway spruce and subsequently European ash were the most admixed tree species. However, both species are currently highly endangered in Europe, either by bark beetle outbreaks or by the fungal pathogen *Hymenoscyphus fraxineus* (Vacek et al. 2017b; Hlásny et al. 2021).

4.2. Effect of climate factors on growth

The growth chronology of black alder is comparable to other deciduous tree species from Central Europe's temperate forests (Lebourgeois et al. 2005; Rozas 2005). In our case, dendrochronology showed that alder was very sensitive to severe frost at the beginning of the year or extreme climatic weather fluctuations. Similar findings were attained by Douda et al. (2009), who reported that the alder annual ring width was sensitive enough to reflect signals from exogenous factors, especially changes in the groundwater level. However, several dendroclimatological studies have shown a relatively weak relationship between annual radial tree growth and wetland climate (Linderholm 1999; Linderholm & Leine 2004). Alder growth response to climatic factors in our,study plots was in most cases significantly higher in the current compared to the previous year.

Specifically, the temperature was important for the successful radial growth of black alder in a numberyof our plots in Eurasia, primarily between February and June of the current year, with March being the main month influencing growth. Similarly, Vacek et al. (2016) reported that temperature in January, March, May, and August of the current year positively influenced the radial growth of alder stands in mountainous areas of the Czech Republic. A less pronounced effect on radial growth was found for monthly precipitation. A more significant negative effect of precipitation on the radial growth of black alder in our plots was demonstrated in May of the previous year (spring snowmelt), and in August of the current year (summer storms and floods). However, the most significant was the prevailing positive relationship in February of the current year (sufficient snow cover or precipitation in general). The low influence of precipitation on growth in wetland and peatland habitats is documented in numerous studies, e.g., for Norway spruce (Vacek et al. 2015; Král et al. 2015; Putalová et al. 2019). By contrast, at some study sites, the dependence of radial increment on temperature (GBR 230, CZE 645, POL 85) or precipitation (GBR 230, SVK 290, TUR 395) was not demonstrated at all. These findings are consistent with the claims of Laganis et al. (2008) that radial growth is relatively independent of temperature and precipitation fluctuations.

Alder growth is strongly influenced by several local and regional environmental variables. In studies focusing on vegetation-environment relationships, local factors have often been discussed, including physical and chemical properties of the soil and groundwater level fluctuations (Härdtle et al. 2003; Herault & Honnay 2005; Douda et al. 2009; van der Maaten et al. 2015;

Slezák et al. 2017). The landscape configuration, altitude, and associated climatic factors, etc., are highly relevant (Douda 2010; Slezák et al. 2014; Pielech 2015; Pielech et al. 2015). In our study, it was shown that the effect of temperature on growth changes significantly from negative to positive with increasing altitude. For example, in the study plots in Turkey, the temperature had a negative effect in one month in the lowest plot (TUR 205), while in the highest plot (TUR 1015), four months with a positive correlation between temperature and growth were found. Sariyildiz (2015) reported that temperature is a significant determinant in the rate of decomposition in the soil and also for the growth in tree species including black alder especially on higher elevations in the Black Sea Region of Turkey. For precipitation, an opposite, but not as pronounced, a trend was found. In general, low temperatures in upland areas and a lack of precipitation in lowland areas are limiting factors for the tree growth, and vice versa (Mäkinen et al. 2002; Zhang et al. 2012).

4.3. Relationship between growth and geographical setting

Numerous studies (Meko 2006; Quinn & Sellinger 2006; Wiles et al. 2009; DeRose et al. 2014) have shown that groundwater level fluctuations around lakes are only partially related to the growth of alder and other tree species in the riparian zone. Invariably, this depends on regional climate, groundwater level, vegetation, land use, and especially geographic location (Adrian et al. 2009; Webster et al. 2000). In our case, latitude played a significant role in terms of alder radial growth when compared to longitude, with the highest influence found for altitude. The importance of the influence of the north-south direction on radial growth has also been documented for other tree species (Mäkinen et al. 2002; Huang et al. 2010). In addition, differences in the substrate (organic vs. mineral) may influence alder growth (van der Maaten et al. 2015) and our study shows that a wide range of soil types and geological bedrock were present in the study plots. Similarly, previous land use may have a significant influence on alder radial growth, which is very closely related to nutrient availability and quantity, as has been confirmed, for example, for Norway spruce (Bartoš & Kacálek 2011; Cukor et al. 2019).

For the reasons mentioned above, the response time to alder growth can vary strongly, resulting in complex interactions with riparian stand growth (van der Maaten et al. 2015). Precipitation anomalies can have direct effects on alder growth, but also indirect ones through delayed effects even over several years (Argyilan & Forman 2003). It always depends on the adaptive responses of alder to climate change in given environmental conditions. In our research, we found that the sensitivity of precipitation to radial growth decreases not only with increasing altitude, but also with the increasing stand age. Alder individuals which hasve a heart root system (Claessens et al. 2010) can tap into deeper horizons with age where trees find a greater availability of soil water. This may decrease their dependence on precipitation. In dry years, alder can form narrow rings because its roots are vulnerable to drought, especially in lowlands (Hacke & Sauter 1996). On the other hand, excessive groundwater levels in flood areas can also subject alder to stress that can also lead to narrowing of the annual rings (Laganis et al. 2008; Elferts et al. 2011; Rodríguez-González et al. 2014), for example, by inducing hypoxic conditions that progressively inhibit tree growth (Kozlowski & Pallardy 1997). Generally, in terms of climate change, riverside sites with the mixing of other tree species seems to be the most stable for alder stands compared to marshy and plateau sites with high soil moisture that are typically the three main sites for alder according to Claessens (2003). Vacek et al. (2016) documented lower growth variability in riparian alder stands compared to drier sites, similar to our study. Moreover, as with other tree species (Kramer et al. 2010; Dulamsuren et al. 2017), it can be expected that the alder stands will gradually spread to upper altitude-upper areas and to the north while declining in the south and lower altitudes.

5. Conclusion

Black alder is one of the important broadleaved tree species in Eurasia, primarily from the aspect of nature conservation of specific water-influenced habitats. Therefore, the understanding of the impact of climatic conditions on the growth of this tree species is among crucial factors for forest management in future decades. According to our findings, the air temperature has a significantly higher effect on the radial growth of alder compared to precipitation, especially in March of the current year. The relationships with radial growth and the monthly sum of precipitation are less significant, with February being the most significant month affecting the diameter increment. The variability of alder growth since the second half of the observed period (1995–2015) was significantly increasing together with the occurrence of NPYs characterizing extremely low diameter increment. A significant decrease in radial growth occurs due to ongoing climate change, especially extreme weather fluctuations, strong frosts, and more frequent drought periods, which may be related to a decrease in groundwater level. From a geographical point of view, latitude has a higher effect on the alder growth when compared to longitude. However, the most important parameter affecting its radial growth is altitude. Moreover, the effect of temperature on the increment is negative in the lowlands and changes to positive with an increase in altitude. Nevertheless, the production of alder stands is significantly influenced by several local and regional environmental variables, often frosts, flood zones, etc., which significantly affect radial growth. Due to the considerable variability of regional factors on the radial growth of alder, no precise and unambiguous conclusion can be reached regarding the influence of climatic factors in changing environmental conditions. Therefore, it is important to continue research with a focus on long-term groundwater monitoring.

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