ORIGINAL PAPER

Does leaf mass per area (LMA) discriminate natural pine populations of different origins?

Włodzimierz Buraczyk[1] · Mirela Tulik[2] · Agata Konecka[1] · Henryk Szeligowski[1] · Marcin Czacharowski[1] · Mateusz Będkowski[1]

Abstract

Tree provenance trials are believed to be a valuable tool for assessing the adaptive potential of a population to a changing environment and ultimately for predicting the populations that are best adapted to global warming. Here, the phenotypic plasticity of morphometric traits of needles and lateral shoots of pines growing in a provenance plot in central Poland was examined to assess the inter- and intra-population variability. No significant differences were found in the measured and counted morphometric features, i.e., needle length (NL), cumulative needles length (CNL), thickness (ST), volume (SV) and shoot density (SD), number of needles per 5 cm fragment of shoot (NN), dry weight of needles (NDW) and shoot (SDW), thickness of bark (BT) and wood (WT), pith diameter (PD), and needle dry mass per area (LMA) among three pine populations while accounting for their region of origin (inter-population variability). In terms of the above-mentioned features, individual populations differed significantly from each other, except for NN and ST. We also noticed a positive, significant relationship between LMA and ST in all studied populations and based on Euclidean distances of measurable or counted traits, three population groups were identified. We concluded that LMA, which is commonly used to quantify leaf structure, is helpful in differentiating intra-population variability.

Introduction

While there have been some previous studies on tree responses to global warming, they are still not sufficient to predict tree growth reactions in warming conditions, especially in boreal and temperate climates (Matala et al. 2006; Schulze et al. 2006; Reich and Oleksyn 2008; Way and Oren, 2010). Temperature and rainfall are among the factors changing as a result of global warming, due to an increase in greenhouse gas emissions, which influence the incidence and growth of trees (Hansen et al. 2001; Morecroft

and Paterson 2016). Therefore, it is assumed that reducing water availability will result in a decline in the productivity of forest ecosystems. It is known that reduced water availability or dry conditions alter tree traits, *inter alia*, morphology, anatomy, and chemistry of a leaf due to the existence of an active interface between the forest ecosystem and the atmosphere (Hansen et al. 2001; Niinemets 2001; Wang et al. 2012; Wyka et al. 2012; Neyret et al. 2016; Galdina and Khazova 2019). These adaptive modifications of leaf attributes, which are observed depending on changing environmental conditions, are usually treated as a part of the strategy that allows trees to occupy different environmental sites (Soethe et al. 2008; Poorter et al. 2009; Wang et al. 2017).

Key functional (ecophysiological) predictors usually include leaf size, which determines water use efficiency and the amount of light captured for photosynthesis (Xu et al. 2009; Whitman and Aarssen 2010; Zhang et al. 2016), as well as leaf mass per area (LMA) or its inverse-specific leaf area (SLA, the ratio between leaf area and leaf dry

✉ Mirela Tulik
   mirela_tulik@sggw.edu.pl

1 Department of Silviculture, Warsaw University of Life Sciences, Nowoursynowska 159, 02-776 Warsaw, Poland

2 Department of Forest Botany, Warsaw University of Life Sciences, Nowoursynowska 159, 02-776 Warsaw, Poland

mass), that are used to correlate capture of light and tree growth (Poorter and Remkes 1990; Cornelissen et al. 1996). Cunningham et al. (1999) stated that the above-mentioned features show the potential return on investment in a leaf for light capture, e.g., SLA increases with decreasing dry matter allocation to leaf tissue for a given leaf area. LMA or its inverse are believed to be variable between species (Kazakou et al. 2014) and environmental parameters (Poorter et al. 2009). Species-level LMA has been shown to increase with latitude (Hulshof et al. 2013), altitude (Rajsnerová et al. 2015), and insolation (Ackerly 2004; Larcher et al. 2015) as well as diminish with rainfall (Warren et al. 2005). LMA is also significantly higher in isolated trees than in forest edge or forest understorey (Sprugel et al. 1996; Wang et al. 2006). Moreover, intra-individual variation in LMA value has also been observed (e.g., 26% of the total variation, Shipley 1995) which is a result of the branch position in the canopy (Bruschi et al. 2003). In the same tree, the shaded leaves have lower LMA compared with sunny leaves (Bruschi et al. 2003). It is assumed that larger LMA is a result of the greater thickness of leaf lamina or tissue density through increased cell wall lignification or decreased fraction of intercellular spaces (Witkowski and Lamont 1991; Hassiotou et al. 2010; Wyka et al. 2012; Villar et al. 2013). Poorter et al (2009) stated that woody species have higher LMA than herbaceous plants, and conifers have a higher LMA than deciduous trees. LMA is higher in saplings that bear mature needles than in seedlings with mostly juvenile needles (heteroblasty; Han et al. 2008). Moreover, in field conditions, species have higher LMA than in laboratory conditions, which is usually caused by higher insolation. Most often, however, it is the genetic factor that determines the specificity of features such as leaves or the different growth reactions in individual populations (Giertych 1979; Repo et al. 2000).

The specific responses of populations to environmental factors, including climate, are usually assessed by common garden experiments. These experiments provide valuable information for foresters on the survival rate and phenotypic plasticity of trees which allow one to select populations within a species best adapted, productive, and are not prone to biotic and abiotic stresses (White et al. 2007). One such provenance plot has been established in 1966 in central Poland, where the offspring of 16 Polish populations of Scots pines (*Pinus sylvestris* L.) are growing. The morpho-anatomical needle traits of pines growing there have been investigated by Zajączkowska et al. (2020). They found that pines from these populations differ in terms of the analyzed needle attributes (i.e., needle length and thickness, the length of the membranous scale at the base of the needle, the number of resin ducts, the thickness of the epidermis, the distance between the vascular bundles, and the cross-sectional area of the

transfusion tissue), however, the differences, for individual traits, were small and in most cases were statistically insignificant. Despite the slight differences between the studied populations, it was possible to separate the geographically studied populations into three groups, namely: central-western, north-eastern, and south-eastern. Additionally, Łabiszak et al. (2017) found variability of morphological needle traits of Scots pine among populations from mountain and lowland areas of Poland. The differentiation both among the population and within the population of each of the examined features of *P. yunnanensis* needles and cones was demonstrated by Xu et al. (2016). In turn, Poljak et al. (2015), investigating the morphological variability of *Sorbus domestica* leaves in Croatia, showed differences between trees within the population, as well as differences between populations. It is a fact that the morphological features of a tree and its organs are important for the differentiation of individuals (Violle et al. 2007) when accounting for life cycles, ecological, and geographic distributions (Gill et al. 2002; Wahid et al. 2006) as well as evolutionary aspects and conservation status (Kaplan, 2001; Gregorius et al. 2003).

The adaptive abilities of trees along with the use of long-term provenance experiments (Aitken et al. 2008; Chakraborty et al. 2015, 2016; Kijowska-Oberc et al. 2020) allowed to determine the inter- and intra-population variability with respect to morphometric traits of the needles and the shoots collected from pines growing at the experimental plot in central Poland.

As the offspring of selected populations grow in homogeneous soil, topography, and under the same climatic conditions, it is believed that the diversity of the analyzed features will be the cause of heritable genetic variation. Further, our results on the morphometric traits of the assimilation apparatus and, in particular, the characteristics of the structural parameter as LMA will provide prognostic tools for inferring the potential growth rate of pine populations on provenance trials. Our results may also be useful for forecasting the directions of natural and assisted migration of the population of woody species under the conditions of climate change.

Materials and methods

The research material was collected from the population of 50-year-old Scots pines (*P. sylvestris* L.) growing at the experimental plot at the Forest Experimental Station of the Warsaw University of Life Sciences in the Rogow Forest District (central Poland, 51°54′29.1″N, 19°54′46.4″E). The experimental plot was established in 1966, on post-agricultural land, in a system of 5 repetitions (blocks) of

one-year-old seedlings that were the offspring of 16 Polish populations of Scots pine. In 1966, the habitat was defined as a fresh mixed coniferous forest, and after the revision of the management plan in 1989, it was reclassified as a fresh mixed forest (Zielony 1993).

The experimental plot is located at an elevation of 160 m above sea level. The soil is strongly acidic up to a depth of 160–180 cm (Szeligowski et al. 2015). For this region, the rainfall is low (579 mm/year) with an average annual temperature of about 7.8 °C.

Our trial covered 9 of the 16 national populations located there and represented the three primary regions of Scots pine locations in Poland. These populations have been assigned the following codes: 1—Rogow, 2—Bolewice, 3—Janów Lubelski, 4—Rospuda, 6—Spala, 8—Karsko, 9—Starzyna, 11—Gubin, 14—Taborz (Table 1). In 2016, from every individual population, 13 trees were harvested as part of thinning procedure. Trees had a comparable total height (they represented the highest biosocial positions—class II according to Kraft's classification). Their diameter was measured at the breast height (DBH) and DBH cross-sectional area (B 1.3 m^2) was calculated for every tree. Then, from the last whorl of every cut tree, 3 one-year-old lateral shoots with needles were collected. The research material consisted of a 5-cm fragment of shoots with needles cut off at a distance of 3 cm from the bud. From every 5-cm fragment of the shoot, pairs of needles were separated and counted. If there were more needle scars on the shoot than the number of needles, the "gaps" were filled with the nearest needles from outside the fragment. Then, the scans of 10 pairs of needles, 5-cm fragment of shoots, and their cross-sections were made (Fig. 1) with a resolution of 1200 dpi using the Epson Expression 12000XL scanner. The obtained images were saved as BMP files to measure (i) length and thickness of needles, (ii) thickness of 5-cm shoot fragments in the middle of their length, and (iii) cross-sections via shoots

Fig. 1 An example of the research material used in our analysis

to determine the thickness of pith, wood, and bark with the use of CooRecorder 9.3.1. In turn, the length (at the edge of the needle) and the thickness of the needle we measured using the WinSEEDLE ™ 2017. Then, all the shoots' fragments and needles we dried at 104° C for 24 h (Memmert forced air dryer: type UF110, Producer GmbH + Co.KG). After the drying process was completed, the shoots and needles were weighted on a laboratory scale (PRECISA BALANCES, Type 160 M) in order to determine their dry weight. The dry weight measurement was performed with an accuracy of 0.001 g.

Moreover, the cumulative length of needles was calculated, which we defined as the product of the number of needles on a 5-cm fragment of the shoot and their average length. This parameter was counted as it determines the size of the active surface of the needles on the examined fragment of the shoot. This is due to the fact that both the length and the number of needles have a direct impact on the size of the assimilation apparatus. The measurement

Table 1 Localization of Scots pine populations in Poland (mother stands) from which the seeds were collected and used to design a provenance plot in Rogow Forest District

Population number	Population name	Geographic coordinates		Height above mean sea level (AMSL, m)
		Latitude N	Longitude E	
1	Rogow[C]	51°49′	19°53′	190
2	Bolewice[W]	52°23′	16°10′	90
3	Janow Lubelski[C]	50°40′	22°25′	250
4	Rospuda[N]	53°55′	22°55′	205
6	Spala[C]	51°35′	20°15′	150
8	Karsko[W]	52°54′	15°15′	75
9	Starzyna[N]	52°38′	23°37′	170
11	Gubin[W]	51°55′	14°50′	70
14	Taborz[N]	19°55′	19°55′	110

[C]populations from central region, [N]populations from northern region, [W]populations from western region

data also allowed us to determine the value of the LMA (leaf mass per area—LMA) index, which defines the relation of the dry weight of needle per its surface. For every tree, the average LMA index was calculated based on 12 needles, for a population it was expressed as the mean LMA of trees within every population, and for regions as the mean LMA of three populations in every region. Additionally, we calculated the density of a 5-cm fragment of shoot as the ratio of the dry mass of the shoot per its volume.

The obtained values of morphometric features of needles and fragments of pine shoots from the population were averaged, and then their linear relationship with the LMA coefficient was determined. For this purpose, the Pearson linear correlation coefficient r was used, and the statistical significance level p was determined at $\alpha = 0.05$.

All data we obtained were tested for normality using a Shapiro–Wilk test. In order to determine the statistical significance of the differences between the average characteristics of the needles and shoots from selected populations, a one-way ANOVA analysis of variance for a random block layout was used at $\alpha = 0.05$. In used model, trees were treated as the repetitions. The one-way ANOVA we also used to reveal statistical differences between the mean characteristics of needles and shoots in regions (central, southern, and western). In that case, the repetition was the mean value of needles and shoots traits in every population. If the result

of the analysis of variance allowed to reject the hypothesis about the lack of differences between the populations, Tukey's post hoc test we used.

Additionally, for the purpose of identifying a multi-features similarity between the populations, the Ward's cluster analysis method, and the Euclidian distance square was used. The calculations were performed using the statistical package Statistica 13.3 and Statgraphics 17.

We have shown the analyzed pine attributes graphically both for every surveyed population and for the regions they represent including the central (Rogow, Spala, Janow Lubelski), northern (Taborz, Rospuda, Starzyna), and western (Karsko, Bolewice, Gubin) regions.

Results

There were no significant differences between Scots pines from the three regions of Poland in terms of the measured and calculated morphometric features, i.e., diameter at breast height (DBH), DBH cross-sectional area (B 1.3 m^2), needle length (NL), cumulative needles length (CNL), thickness (ST), volume (SV) and density (SD) of shoot, number of needles per 5-cm shoot fragment (NN), dry weight of needles (NDW) and shoot (SDW), bark (BT) and wood (WT) thickness and pith diameter (PD) as well as the LMA coefficient (Table 2).

Table 2 The attributes of needles and shoots of Scots pines from three regions of Poland

Measured and calculated attributes	Region of Poland			Average	*p*-value
	Central	Northern	Western		
DBH (mm)	220	222	232	225	0.422
B 1.3 (m^2)	0.0385	0.0390	0.0426	0.0401	0.946
Needle length (NL, mm)	64.1	65.4	65.4	65.0	0.879
Cumulative needles length (CNL, mm)	2224	2269	2240	2244	0.908
Needles number (NN, no./5 cm-shoot fragment)	35.2	35.0	34.5	34.9	0.837
Dry weight of needles (NDW, g/5 cm-shoot fragment)	1.823	1.727	1.729	1.758	0.837
Shoot thickness (ST, mm)	5.39	5.29	5.54	5.42	0.746
Shoot volume (SV, cm^3)	1.190	1.142	1.250	1.197	0.723
Shoot density (SD, g cm^{-3})	0.422	0.431	0.371	0.406	0.765
Dry weight of shoot (SDW, g)	0.435	0.428	0.403	0.421	0.782
Bark thickness (BT, mm)	1.78	1.77	1.88	1.81	0.527
Wood thickness (WT, mm)	2.04	1.95	2.06	2.02	0.362
Pith diameter (PD, mm)	1.51	1.44	1.51	1.49	0.799
Leaf mass per area (LMA, mg cm^{-2})	15.70	14.45	14.45	14.93	0.071

p-value shows differences between the averaged values of the analyzed features of pines from three regions of Poland

Table 3 Statistical characteristics of the LMA coefficient of nine Scots pine populations

Population	LMA (mg cm^{-2})			SD	p_1-value
	Mean	Max	Min		
Bolewice[W]	14.3	17.3	11.4	1.3	0.0003
Gubin[W]	15.2	18.7	10.9	2.2	0.0000
Janow Lub.[C]	16.6	32.1	11.0	5.9	0.0000
Karsko[W]	13.9	19.4	10.8	1.8	0.0002
Rogow[C]	15.6	19.7	13.0	1.8	0.0000
Rospuda[N]	14.9	18.6	11.7	1.7	0.0019
Spala[C]	15.0	21.4	11.2	2.3	0.0000
Starzyna[N]	14.8	24.9	11.2	2.7	0.0001
Taborz[N]	14.3	17.2	12.3	1.2	0.0935
Mean	14.9				–
p_2-value	0.3077				

Max, Min—maximum and minimum values, SD—standard deviation

p_1-value—level of statistical significance between the mean LMA of trees in each population

p_2-value—level of statistical significance between mean values of LMA population

[C]populations from central region, [N]populations from northern region, [W]populations from western region

The value of the LMA ranged from 13.9 mg cm^{-2} for the Karsko population to 16.6 mg cm^{-2} for the Janow Lubelski population, with the mean calculated for all populations being 14.9 mg cm^{-2} and an insignificant difference between the population means ($p = 0.3077$). We found significant differences in LMA within the population, with the exception of that in Taborz. The highest LMA value (32.1 mg cm^{-2}) for a single tree was revealed in Janow Lubelski population, while the lowest (10.8 mg cm^{-2}) was found in Karsko population (Table 3). In terms of the above-mentioned features, the individual populations differed significantly from each other, except for NN, ST and BT, ($p = 0.1083$, $p = 0.0774$, and $p = 0.3989$, respectively; Fig. 2).

The pines from Spala and Starzyna had the longest needles (almost 70 mm each), and the shortest needles had those from Rogow (55 mm) and Gubin populations (approx. 60 mm; Fig. 2). In the case of NDW, the highest value was recorded in the population from Spala and Karsko, and the lowest NDW in the population from Rogow. The pine populations from Karsko, Janow Lubelski, and Starzyna had the highest SDW (0.47 g every), while Gubin

and Rogow had the lowest SDW, 0.33 g and 0.35 g, respectively (Fig. 2).

The rectilinear relationships between LMA and other features measured or counted were varied and the vast majority of correlations were positive and statistically significant (Table 4). In the case of the population from Gubin, 10 out of 11 analyzed features showed a positive, significant correlation. Furthermore, the statistical significance between LMA and CNL was found only in Gubin population. A large number of positively correlated traits (eight and more) was also noted in the populations of Rospuda, Spala, Karsko, Janow Lubelski, and Taborz. In the above-mentioned populations, an increase in the LMA coefficient resulted in an increase in ST and SDW, as well as BT, WT and PD (Table 4). Only in the case of the population from Bolewice, the relationship between LMA and SDW was statistically insignificant ($r = 0.168$). For all tested populations, the statistically significant relationships were found between LMA and NDW, ST, SV (Table 4).

Using the cluster analysis, we identified three groups: one was represented by the populations from Rogow and Gubin. The second group included 4 populations: Bolewice, Karsko, Rospuda, and Taborz. The third group consisted of Janow Lubelski, Spala, and Starzyna (Fig. 3; Table 5).

Discussion

The phenotypic plasticity of an organism, the ability of the genotype to produce distinct phenotypes as a result of environmental stresses, is thought to play a key role in the process of the organism's adaptation to the environment (Chevin et al. 2010; Fox et al. 2019). In the provenance experiment, selected morphometric features of Scots pine organs representing three origins were examined, which gives us the basis for determining the variability of the population and identifying their features under strong genetic control (Hebda et al. 2017; Lesiczka et al. 2017). Among the many morphometric features, we put our attention on LMA, which quantifies how much biomass a tree has invested in one unit of the photosynthetically active surface. High LMA is believed to be a good indicator of conservative ecological strategy and is a general feature of leaves from unproductive or stressful environments (Reich, et al. 1997; Wright et al. 2004). The LMA of most terrestrial species ranges from 30 to 330 g m^{-2} (3–33 mg cm^{-2};
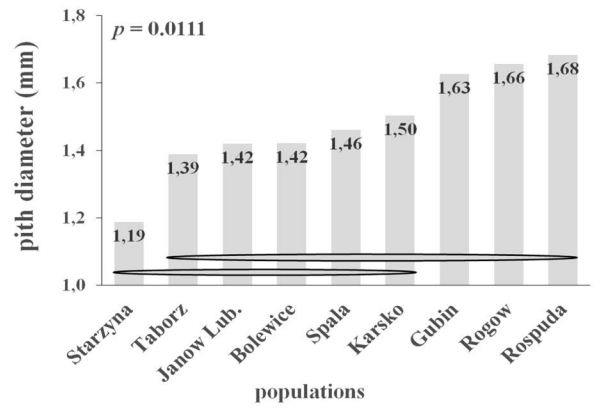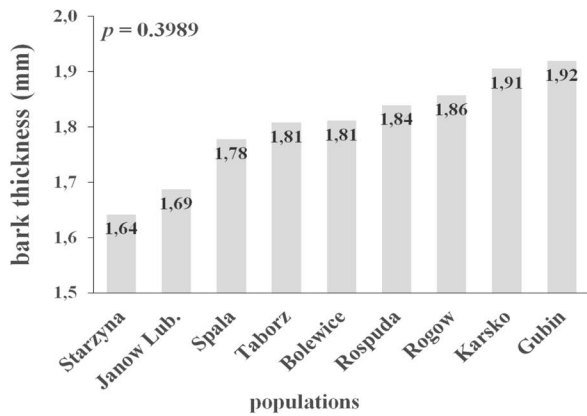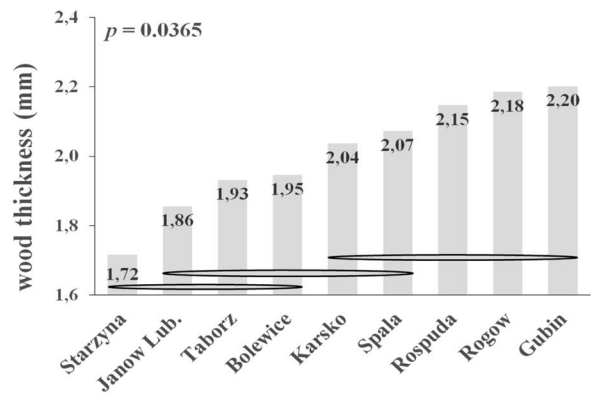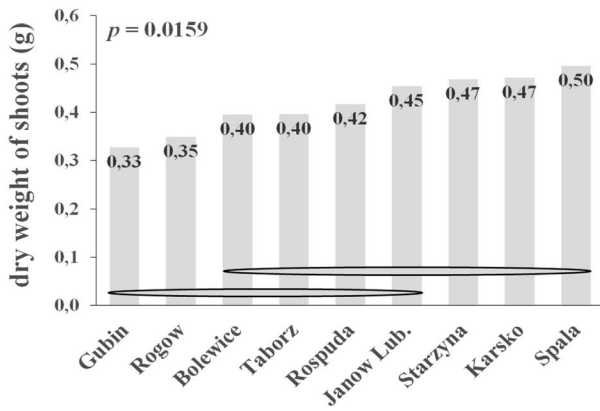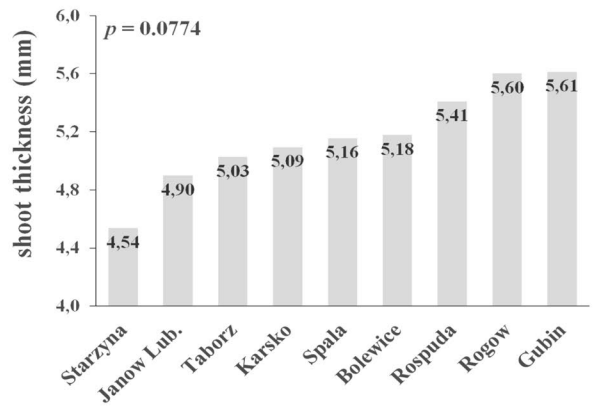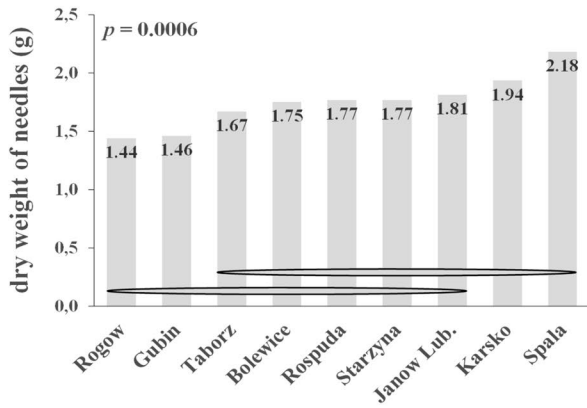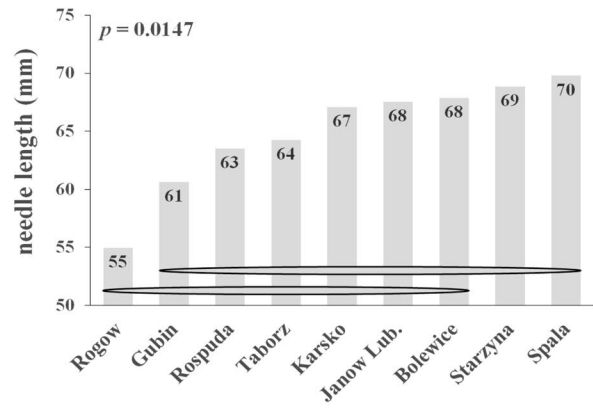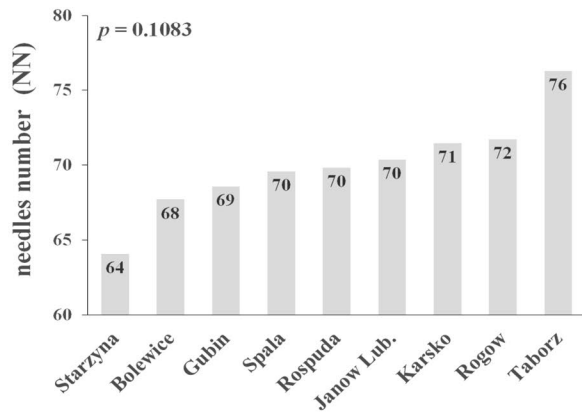
◄**Fig. 2** Characteristics of analyzed features of the needles and shoots of nine Scots pine populations (horizontal bars in graphs represent statistically homogeneous groups calculated using the Tukey's test at the level of $\alpha = 0.05$)

Poorter et al., 2009). Chen et al. (2014) stated that LMA can be expressed as a linear function of light, and it reaches about 12.64 mg cm^{-2} for conifer species when light is above ca 30%. A higher value of LMA has also been found in shorter and long-lived needles of pines as a result of an adaptation to a cold environment (Jankowski et al. 2017). LMA values for the studied populations and regions are in the LMA ranges given for conifers, in accordance with the literature. In our research, the region of central Poland was characterized by the highest LMA value when compared to the northern and western, although these differences were statistically insignificant. However, this feature allowed us to determine significant intra-population variability. The highest LMA value was calculated for the population from Janow Lubelski, a part of Poland with colder winters than in the western part (Chojnacka-Ożga and Ożga 2018), and for the population of pines from Rogow, which had the shortest and lightest needles. Therefore, we suppose that LMA values are a feature that may express adaptation to low temperatures (Janowski et al. 2017), and probably reflects strong lignification of the wall of needles cells, which is supported by the literature (Niinemets et al. 2004; Larcher 2005) as LMA is generally a product of leaf thickness and leaf density (Niinemets 2001). Padros et al. (2014) also reported that high LMA partially explains higher tolerance to low temperature within a given species.

It seems, therefore, that the significant intra-population variability in terms of LMA may be considered, in a possible economic selection, based on the efficiency of carbon fixation by trees and thus their adaptability to unfavorable environmental factors. Such a statement is consistent with literature reports because leaves with a high LMA are long-lived, avoided by herbivores, and preserve the captured nutrients and carbon more efficiently (Peréz-Harguindeguy et al. 2003). Plants with high LMA not only have long-lived leaves, but also the root vitality is greater (Ryser 1996), and these features give an advantage in competitive conditions.

Urbaniak et al. (2003) while examining the morphological features of the needles of Scots pine populations from different habitats, showed stable needle features with little inter-individual variability such as number of stomata on adaxial and abaxial sides of the needle and those with the greatest variability such as needle length and number of stomatal rows on the abaxial and adaxial sides of the needle. The features that significantly

Table 4 Correlation coefficients (r) describing the relationship between LMA and the characteristics of needles and shoots of Scots pine populations

Variables		The value of the correlation coefficient r calculated for the population								
X	Y	Rogow[C]	Bolewice[W]	Janow Lub.[C]	Rospuda[N]	Spala[C]	Karsko[W]	Starzyna[N]	Gubin[W]	Taborz[N]
LMA (mg cm^{-2})	Needle length (NL, mm)	0.169	0.322*	−0.016	0.471**	0.382*	0.298*	0.250	0.687**	0.460**
	Cumulative needles length (CNL, mm)	−0.001	−0.280	−0.276	0.214	0.020	−0.114	0.131	0.477**	0.244
	Needles number (NN, no./5 cm-shoot fragment)	−0.239	−0.555**	−0.341*	−0.365*	0.347*	−0.468**	−0.251	−0.536**	−0.147
	Dry weight of needles (NDW, g)	0.644**	0.582**	0.687**	0.810**	0.783**	0.582**	0.690**	0.833**	0.571**
	Shoot thickness (ST, mm)	0.497**	0.402**	0.495**	0.419**	0.814**	0.638**	0.561**	0.623**	0.675**
	Shoot volume (SV, cm^3)	0.667**	0.462**	0.765**	0.537**	0.768**	0.612**	0.416*	0.605**	0.759**
	Shoot density (SD, g cm^{-3})	0.139	0.140	0.672**	−0.060	−0.069	−0.263	−0.103	0.170	−0.087
	Dry weight of shoot (SDW, g)	0.498**	0.168	0.416*	0.445**	0.715**	0.433**	0.348*	0.517**	0.701**
	Bark thickness (BT, mm)	0.279	0.486**	0.381*	0.733**	0.601**	0.454**	0.281	0.603**	0.623**
	Wood thickness (WT, mm)	0.577**	0.204	0.447**	0.335*	0.585**	0.399**	0.158	0.358*	0.688**
	Pith diameter (PD, mm)	0.169	0.322*	−0.016	0.471**	0.382*	0.298*	0.250	0.687**	0.460**

*statistically significant relationship at $\alpha = 0.05$, **statistically significant relationship at $\alpha = 0.01$.

[C] populations from central region, [N] populations from northern region, [W] populations from western region
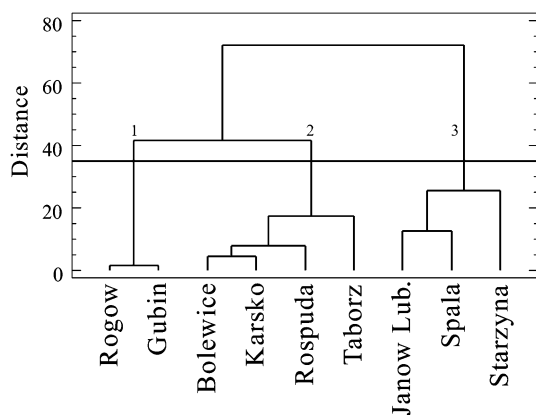
Fig. 3 Dendrogram of pine populations constructed by the Ward's clustering method

differentiated the individuals were the length of the needle. In our study, we did not find a significant difference in needle length (NL) among the populations, but individual populations differed significantly from each other, which is consistent with Zajączkowska's research (Zajączkowska et al. 2020). The NL for individual populations ranged from 55 to 70 mm and these values are within the range given for pines in Poland (Urbaniak and Karliński 2001; Urbaniak et al., 2003). It is, however, a surprise to us that the population from Spala had only a slightly lower LMA than that from Rogow, but the pine needles from Spala were 15 mm longer when compared to Rogow. Both mentioned populations represent the central region of Poland. Further, for the Rogow population, the relationship between LMA and NL is negligible, while a significant correlation exists for the population from Spala. Moreover, a significant, positive correlation between NL and LMA was also found for all populations from the western part of Poland (Bolewice, Karsko, Gubin), for two populations representing the northern

part (Rospuda and Taborz) and for only one from central Poland (Spala). We assume that NL, apart from other morphometric features, is a genetically controlled feature, as previously reported in earlier studies (Urbaniak et al. 2003; Lesiczka et al. 2017). It also seems that both morphometric (NL) and structural (LMA) traits are well suited for provenance studies as both climatic conditions are the same and needles selected for the tests were also of the same age. An interesting observation seems to be the positive significant relationship between the LMA and the thickness of the shoot that was noted for all studied populations. Perhaps it is related to the storage of starch in the parenchymatic cells of the shoot tissues, however, little is known overall about the effect of sugars in leaf tissues on LMA (Poorter et al. 2009).

The provenance trials usually show that the populations of Scots pine growing in Poland in relation to the most important growth features as total height, DBH, wood mass production per 1 ha, and qualitative features as stem straightness, branch thickness, canopy shape, angle of the branches do not always show statistically significant differentiation (Barzdajn et al. 2016; Hebda et al. 2017). Conversely, these studies show high variability within each population, i.e., between trees. The presented research on needles and shoots traits partially confirms these results, especially in relation to the designated large geographic areas, differentiated in terms of climate, called regions (northern, central, and western). Our results also indicate that differences in LMA, which are considered an ecological indicator, in addition to measurable leaf characteristics, can be used to determine intra-population variability resulting from leaf-environment relations, especially when all these progenies grow under the same environment and are of the same age. The variability of needle and shoot traits shown in our research seems to be useful in tree improvement programs through selection and breeding approaches to advance the development of future generations. Studies

Table 5 Average characteristics of Scots pine needles and shoots clustered according to their multi-features similarity

Clusters of populations	NN	NL	NDW	LMA	SDW	SD	WT	BT	PD
1. Gubin, Rogow	69.64	67.15	1.94	15.24	0.48	0.31	2.18	1.87	1.66
2. Rospuda, Bolewice, Karsko, Taborz	69.73	65.09	1.67	14.18	0.40	0.41	1.98	1.85	1.44
3. Janow Lub., Spala, Starzyna	69.87	62.75	1.72	15.46	0.39	0.51	1.89	1.71	1.36

NN, NL, NDW, LMA, SDW, SD, WT, BT and PD are described in Tables 2 and 4

of the correlation of various traits at the phenotypic level provide the basic knowledge of associations to develop an effective breeding strategy to obtain higher productivity through indirect selection.

Declarations

References

Ackerly D (2004) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. Ecol Monogr 74:25–44

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. Evol Appl 1:95–111. https://doi.org/10.1111/j.1752-4571.2007.00013.x

Barzdajn W, Kowalkowski W, Chmura DJ (2016) Variation in growth and survival among European provenances of *Pinus sylvestris* in a 30-year-old experiment. Dendrobiology 75:67–77. https://doi.org/10.12657/denbio.075.007

Bruschi P, Grossoni P, Bussotti F (2003) Within- and among-tree variation in leaf morphology of *Quercus petraea* (Matt.) Liebl. natural populations. Trees 17:164–172. https://doi.org/10.1007/s00468-002-0218-y

Chakraborty D, Wang T, Andre K, Konnert M, Lexer MJ, Matulla Ch, Schueler S (2015) Selecting populations for non-analogous climate conditions using universal response functions: the case of douglas-fir in central Europe. PLoS ONE 10:1–21. https://doi.org/10.1371/journal.pone.0136357

Chakraborty D, Wang T, Andre K, Konnert M, Lexer MJ, Matulla Ch, Weißenbacher L, Schueler S (2016) Adapting Douglas-fir forestry in Central Europe: evolution, application, and uncertainty analysis of a genetically based model. Eur J For Res 135:919–939. https://doi.org/10.1007/s10342-016-0984-5

Chen A, Lichstein JW, Osnas JLD, Pacal SW (2014) Species-independent down-regulation of leaf photosynthesis and respiration in response to shading: evidence from six temperate tree species. PLoS ONE 9:91798. https://doi.org/10.1371/journal.pone.0091798

Chevin LM, Lande R, Mace GM (2010) Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. PLoS Biol 8:e1000357. https://doi.org/10.1371/journal.pbio.1000357

Chojnacka-Ożga L, Ożga W (2018) Air temperature anomalies in experimental forests in Rogow in 1924–2015. For Res Pap 79:37–44. https://doi.org/10.2478/frp-2018-0005

Cornelissen JHC, Castro-Diez P, Hunt R (1996) Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. J Ecol 84:755–756. https://doi.org/10.2307/2261337

Cunningham SA, Summerhayes B, Westoby M (1999) Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. Ecol Monogr 69:569–588. https://doi.org/10.1890/0012-9615(1999)069[0569:EDILSA]2.0.CO;2

Fox RJ, Donelson JM, Schunter C, Ravasti T, Gaitán-Espitia JD (2019) Beyond buying time: the role of plasticity in phenotypic adaptation to rapid environmental change. Philos Trans R Soc B 374:20180174. https://doi.org/10.1098/rstb.2018.0174

Galdina T, Khazova E (2019) Adaptability of *Pinus sylvestris* L. to various environmental conditions. In: conference series: earth and environmental science, vol 316, pp 012002. https://doi.org/10.1088/1755-1315/316/1/012002

Giertych M (1979) Summary of results on Scotch pine (*Pinus sylvestris* L.) height growth in IUFRO provenance experiments. Silvae Genet 28:136–152

Gil L, Climent J, Nanos N, Mutke S, Ortiz I, Schiller G (2002) Cone morphology variation in *Pinus canariensis* Sm. Plant Syst Evol 235:35–5

Gregorius HR, Bergmann F, Wehenkel C (2003) Analysis of biodiversity across levels of biological organization: a problem of defining traits. Perspect Plant Ecol Evol Syst 5:209–218. https://doi.org/10.1078/1433-8319-00035

Han Q, Kawasaki T, Nakano T, Chiba Y (2008) Leaf-age effects on seasonal variability in photosynthetic parameters and its relationships with leaf mass per area and leaf nitrogen concentration within a *Pinus densiflora* crown. Tree Physiol 28:551–558. https://doi.org/10.1093/treephys/28.4.551

Hansen AJ, Neilson RP, Dale VH, Flather CH, Iverson LR, Currie DJ, Shafer S, Cook R, Bartlein PJ (2001) Global change in forests: responses of species, communities, and biomes: interactions between climate change and land use are projected to cause large shifts in biodiversity. Bioscience 51:765–779. https://doi.org/10.1641/0006-3568(2001)051[0765:GCIFRO]2.0.CO;2

Hassiotou F, Renton M, Ludwig M (2010) Photosynthesis at an extreme end of the leaf trait spectrum: how does it relate to high leaf dry mass per area and associated structural parameters? J Exp Bot 61:3015–3028. https://doi.org/10.1093/jxb/erq128

Hebda A, Skrzyszewski J, Wachowiak W (2017) Phenotypic differentiation and genetic background variation of Polish provenances of *Pinus sylvestris* L. Sylwan 161:277–286. https://doi.org/10.26202/sylwan.2016135

Hulshof C, Violle C, Spasojevic MJ, McGill B, Damschen E, Harrison S, Enquist BJ (2013) Intra-specific and interspecific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude. J Veg Sci 24:921–931. https://doi.org/10.1111/jvs.12041

Jankowski A, Wyka T, Żytkowiak R, Nihlgård B, Reich PB, Oleksyn J (2017) Cold adaptation drives variability in needle structure and anatomy in *Pinus sylvestris* L. along a 1.900 km temperate-boreal transect. Funct Ecol 31:2212–2223. https://doi.org/10.1111/1365-2435.12946

Kaplan DR (2001) The science of plant morphology: definition, history, and role in modern biology. Am J Bot 88:1711–1741. https://doi.org/10.2307/3558347

Kazakou E, Violle C, Roumet M-L, Vile D, Kattge J, Garnier E (2014) Are trait-based species rankings consistent across data sets and spatial scales? J Veg Sci 25:235–247. https://doi.org/10.1111/jvs.12066

Kijowska-Oberc J, Staszak AM, Kamiński J, Ratajczak E (2020) Adaptation of forest trees to rapidly changing climate. Forests 11:123. https://doi.org/10.3390/f11020123

Łabiszak B, Lewandowska-Wosik A, Pawlaczyk EM, Urbaniak L (2017) Variability of morphological needle traits of Scots pine (*Pinus sylvestris* L.) among populations from mountain and lowland regions of Poland. Folia For Pol Ser A For 59:134–145. https://doi.org/10.1515/ffp-2017-0013

Larcher L (2005) Climatic constraints drive the evolution of low temperature resistance in woody plants. J Agric Meteorol 61:189–202. https://doi.org/10.2480/agrmet.61.189

Larcher L, Nogueira G, Boeger MR (2015) Morphological plasticity and gas exchange of *Ligustrum lucidum* W.T. Aiton in distinct light conditions. Braz Arch Biol Technol 58:877–885. https://doi.org/10.1590/S1516-89132015060439

Lesiczka P, Pawlaczyk EM, Łabiszak B, Urbaniak L (2017) Variability of Scots pine (*Pinus sylvestris* L.) called Taborz pine (forest district Miłomlyn) expressed in analysis of morphology of needle traits and polymorphism of microsatellite DNA. For Res Pap 78:136–148. https://doi.org/10.1515/frp-2017-0015

Matala J, Ojansuu R, Peltola H, Raitio H, Kellomaki S (2006) Modelling the response of tree growth to temperature and CO_2 elevation as related to the fertility and current temperature sum of a site. Ecol Modell 199:39–52. https://doi.org/10.1016/j.ecolmodel.2006.06.009

Morecroft MD, Paterson JS (2016) Effects of temperature and precipitation changes on plant communities. In: Morison JIL, Morecroft MD (eds) Plant growth and climate change. Blackwell Publishing Ltd, Oxford, pp 146–164

Neyret M, Bentley LP, Oliveras I, Marimon BS, Marimon-Junior BH, Almeida de Oliveira E, Barbosa Passos F, Castro Ccoscco R, Dos Santos J, Matias Reis S, Morandi PS, Rayme Paucar G, Robles Cáceres A, Valdez Tejeira Y, Yllanes Choque Y, Salinas N, Shenkin A, Asner GP, Díaz S, Enquist BJ, Malhi Y (2016) Examining variation in the leaf mass per area of dominant species across two contrasting tropical gradients in light of community assembly. Ecol Evol 6:5674–5689. https://doi.org/10.1002/ece3.2281

Niinemets Ü (2001) Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. Ecology 82:453–469. https://doi.org/10.1890/0012-9658(2001)082[0453:GSCCOL]2.0.CO;2

Niinemets Ü, Tenhunen JD, Beyschlag W (2004) Spatial and age-dependent modifications of photosynthetic capacity in four Mediterranean oak species. Funct Plant Biol 31:1179–1193. https://doi.org/10.1071/FP04128

Padros M, Climent J, Alemida H (2014) The role of developmental stage in frost tolerance of *Pinus pinea* L. seedlings and saplings. Ann For Sci 71:551–562. https://doi.org/10.1007/s13595-014-0361-9

Peréz-Harguindeguy N, Diaz S, Vendramini F, Cornelissen JHC, Gurvich DE, Cabidoet M (2003) Leaf traits and herbivore selection in the field and cafeteria experiments. Austral Ecol 28:642–650. https://doi.org/10.1046/j.1442-9993.2003.01321.x

Poljak I, Kajba D, Ljubić I, Idžojtić M (2015) Morphological variability of leaves of *Sorbus domestica* L. in Croatia. Acta Soc Bot Pol 84:249–259. https://doi.org/10.5586/asbp.2015.023

Poorter H, Remkes C (1990) Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. Oecologia 83:553–559. https://doi.org/10.1007/BF00317209

Poorter H, Niinemetes Ü, Poorter IJ, Wright IJ, Villar R (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytol 182:565–588. https://doi.org/10.1111/j.1469-8137.2009.02830.x

Rajsnerová P, Klem K, Holub P, Novotná K, Večeřová K, Kozáčiková M, Rivas-Ubach A, Sardans J, Marek MV, Peñuelas J, Urban O (2015) Morphological, biochemical and physiological traits of upper and lower canopy leaves of European beech tend to converge with increasing altitude. Tree Physiol 35:47–60. https://doi.org/10.1093/treephys/tpu104

Reich PB, Oleksyn J (2008) Climate warming will reduce growth and survival of Scots pine except in the far north. Ecol Lett 11:588–597. https://doi.org/10.1111/j.1399-3054.2006.00682.x

Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. Proc Natl Acad Sci USA 94:13730–13734. https://doi.org/10.1073/pnas.94.25.13730

Repo T, Zhang G, Ryyppö A, Rikal R, Vuorinen M (2000) The relation between growth cessation and frost hardening in Scots pine of different origins. Trees 14:456–464. https://doi.org/10.1007/s004680000059

Ryser P (1996) The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. Funct Ecol 10:717–723. https://doi.org/10.2307/2390506

Schulze ED, Turner NC, Nicolle D, Schumacher J (2006) Species differences in carbon isotope, specific leaf area and nitrogen concentration in leaves of Eucalyptus growing in common garden compared with along an aridity gradient. Physiol Plant 127:434–444. https://doi.org/10.1111/j.1399-3054.2006.00682.x

Shipley B (1995) Structured interspecific determinants of specific leaf area in 34 species of herbaceous angiosperms. Funct Ecol 9:312–319. https://doi.org/10.2307/2390579

Soethe N, Lehmann J, Engels Ch (2008) Nutrient availability at different altitudes in a tropical montane forest in Ecuador. J Trop Ecol 24:397–406. https://doi.org/10.1017/S026646740800504X

Sprugel DG, Brooks JR, Hinckley TM (1996) Effects of light on shoot geometry and needle morphology in *Abies amabilis*. Tree Physiol 16:91–98. https://doi.org/10.1093/treephys/16.1-2.91

Szeligowski H, Buraczyk W, Drozdowski S, Gawron L (2015) Silvicultural value of Scots pine provenances from Poland on the experimental plot in Rogow. Sylwan 159:997–1007. https://doi.org/10.26202/sylwan.2015050

Urbaniak L, Karliński L (2001) Populations of Scots pine (*Pinus sylvestris* L.) under different abiotic environments: similarities and differences in the expression of phenotypic needle characters. In: third Balkan scientific conference. Proceedings, vol II, Sofia, pp 1997–207

Urbaniak L, Karliński L, Popielarz R (2003) Variation of morphological needle characters of Scots pine (*Pinus sylvestris* L.). Acta Soc Bot Pol 72:37–44. https://doi.org/10.5586/asbp.2003.005

Villar R, Ruiz-Robleto J, Ubera JL, Poorter H (2013) Exploring variation in leaf mass per area (LMA) from leaf to cell: an anatomical analysis of 26 woody species. Am J Bot 100:1969–1980. https://doi.org/10.3732/ajb.1200562

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional. Oikos 116:882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Wahid N, González-Martínez SC, El Hadrami I, Boulli A (2006) Variation of morphological traits in natural populations of maritime

pine (*Pinus pinaster* Ait.) in Morocco. Ann For Sci 63:83–92. https://doi.org/10.1051/forest:20050100

Wang Z, Zhang L (2012) Leaf shape alters the coefficients of leaf area estimation models for *Saussurea stoliczkai* in central Tibet. Photosynthetica 50:337–342. https://doi.org/10.1007/s11099-012-0039-1

Wang T, Hamann A, Yanchuk A, O'Neill GA, Aitken SN (2006) Use of response functions in selecting lodgepole pine populations for future climates. Glob Change Biol 12:2404–2416. https://doi.org/10.1111/j.1365-2486.2006.01271.x

Wang C, Zhou J, Xiao H, Liu J, Wang L (2017) Variations in leaf functional traits among plant species grouped by growth and leaf types in Zhenjiang, China. J For Res 28:241–248. https://doi.org/10.1007/s11676-016-0290-6

Warren CR, Tausz M, Adams MA (2005) Does rainfall explain variation in leaf morphology and physiology among populations of red ironbark (*Eucalyptus sideroxylon* subsp. tricarpa) grown in a common garden? Tree Physiol 25:1369–1378. https://doi.org/10.1093/treephys/25.11.1369

Way DA, Oren R (2010) Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. Tree Physiol 30:669–688. https://doi.org/10.1093/treephys/tpq015

White TL, Adams WT, Neale DB (2007) Forest genetics. Cabi Pub, Wallingford, Oxfordshire

Whitman T, Aarssen LW (2010) The leaf size/number trade-off in herbaceous angiosperms. J Plant Ecol 3:49–58. https://doi.org/10.1093/jpe/rtp018

Witkowski ETF, Lamont BB (1991) Leaf specific mass confounds leaf density and thickness. Oecologia 88:486–493. https://doi.org/10.1007/BF00317710

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Boners F, Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821–827. https://doi.org/10.1038/nature02403

Wyka TP, Oleksyn J, Żytkowiak R, Karolewski P, Jagodziński AM, Reich PB (2012) Responses of leaf structure and photosynthetic properties to intra-canopy light gradients: a common garden test with four broadleaf deciduous angiosperm and seven evergreen conifer tree species. Oecologia 170:11–24. https://doi.org/10.1007/s00442-012-2279-y

Xu F, Guo W, Xu W, Wei Y, Wang R (2009) Leaf morphology correlates with water and light availability: What consequences for simple and compound leaves? Prog Nat Sci 19:1789–1798. https://doi.org/10.1016/j.pnsc.2009.10.001

Xu Y, Woeste K, Cai N, Kang X, Li G, Chen S, Duan A (2016) Variation in needle and cone traits in natural populations of *Pinus yuannanesis*. J For Res 27:41–49. https://doi.org/10.1007/s11676-015-0153-6

Zajączkowska U, Piątkowski M, Dolkin A, Buraczyk W (2020) Diversity of needles structure of the selected Polish populations of *Pinus sylvestris* L. on the experimental plots in the forest experimental station in Rogow. Sylwan 164:842–849. https://doi.org/10.26202/sylwan.2020051

Zhang S, Zhang Y, Ma K (2016) The association of leaf lifespan and background insect herbivory at the interspecific level. Ecology 98:425–432. https://doi.org/10.1002/ecy.1649

Zielony R (1993) Warunki przyrodnicze lasów doświadczalnych SGGW w Rogowie/natural conditions of experimental forests of WULS in Rogow. WULS Pub, Warsaw, Poland