European silver fir – an alternative for the dying Norway spruce in Białowieża Forest?

Aleh Marozau¹ ✉, Miłosz Mielcarek², Grzegorz Krok², Rafał Paluch^{1,3}, Krzysztof Chiliński¹

¹ Białystok University of Technology, Institute of Forest Sciences, 17-200 Hajnówka, Piłsudskiego 1A, Poland, phone: +48 85 6829503, e-mail: a.marozau@pb.edu.pl

² Forest Research Institute, Department of Geomatics, Sękocin Stary, Braci Leśnej 3, 05-090 Raszyn, Poland

³ Forest Research Institute, Department of Natural Forests, Park Dyrekcyjny 6, 17-230 Białowieża, Poland

ABSTRACT

The condition of Norway spruce (*Picea abies* (L.) Karst) in the Białowieża Forest is categorized as a crisis. It is believed that due to the cooling in the Holocene, the then-relict species of the forest, silver fir (*Abies alba* Mill.), disappeared from its ecosystems and then spruce appeared. Today's climate change presents challenges to our civilization, including to forestry. However, there is no information at all about how this affected the silver fir in the Białowieża Forest. In the Polish part of the forest (subcompartment 498 Ci, Białowieża Forest District), for the first time a comprehensive study has been carried out on the condition of mature fir trees planted by man and on their progeny. The results indicate high forestry-taxation indicators of trees, resistance to the abiotic factor and competitiveness. Their constitution corresponds to local environmental conditions. However, the disproportionately small number of adult natural regeneration of old firs indicated some kind of malfunction in the mechanism of natural generational change.

KEY WORDS

artificial origin, old trees, adult generation, trees conditions

INTRODUCTION

The abnormal drying of Norway spruce in the Białowieża Forest (as well as in other regions of Europe) is one of the most acute problems of modern forestry. The main reason for this is global warming (Neuner et al. 2015; Brzeziecki et al. 2018a).

Abies alba is also associated with periods of extinction. For example, the species' total extinction in the mountain and plain forests of the southern Alps oc-

curred in approx. 7300–7000 and 6000 years BCE. This was due to a number of factors (fires, human activities), including climatic changes during the Holocene, which caused a moisture deficit (Wick and Möhl 2006).

It is believed that silver fir is not a species alien to Białowieża Forest. It migrated to its territory along with (*Taxus baccata* L.) presumably in the climatic optimum of the Holocene from the southwest direction (Karpaty, Sudety) through Lubelszczyzna and Płaskowyż Łukowski (Szafer 1920; Paczoski 1930; Dąbrowski

1959). According to Srodoń (1983), its movement began in the sub-boreal and ended in the subatlantic period of the Holocene. At the same time (2000 BCE), a range of *A. alba* (Litkowiec and Lewandowski 2015) was formed on the territory of Poland. Along with pioneer species (birch, pine and aspen), oak and linden were abundantly represented in the Forest with the appearance of silver fir in it (Paczoski 1930). In connection with the cooling that followed, the conditions for *A. alba* worsened and the occupied area decreased to one island area of permanent residence located in the middle of the swamps in the Tisovik tract (Belarusian part of the Forest) (Szafer 1920; Korczyk 2015a). But at the same time, cooling conditions favoured the expansion of the boreal species of Norway spruce over the entire territory of the Forest, which visually adopted the characteristics of a taiga forest (Paczoski 1930).

It is well known that the eastern border of the silver fir range is an area of frosty winters (Jaworski 2011), and most of the modern warming occurs in the cold period (Pomortsev et al. 2015). In this regard, it will be logical to assume that perhaps a favourable period has again arrived for silver fir in forest ecosystems, remote to the north and east of its continuous range, including in the Białowieża Forest. In any event, it was projected that this species in western and central Europe under warming conditions have great potential to thrive (Vittasse et al. 2019).

The qualitative characteristics and quantitative parameters of the subject of the study, represented by old silver fir trees with an age of about 100 years and adult offspring, are a basic indicative assessment of the conformity of growing conditions to the needs of plants. They also make it possible to determine their response to climate conditions in the past and, which is especially important and relevant, in the present. Thus, this is one of the most objective criteria that can be used to justify a decision on the appropriateness of applying practical forestry information obtained in the study of this subject.

In view of the foregoing, we hypothesized European silver fir as a possible alternative to Norway spruce that is drying up immensely. This is probably the first study on the Białowieża Forest, including the Belarusian part, in which a similar hypothesis is put forward. The hypothesis was tested on the basis of the results of a long experiment started in Białowieża Forest by unknown, unfortunately, Polish foresters, at the beginning

of the 20th century and continued by us at the beginning of the 21st century under the conditions of global climate change.

The purpose of the study was to make a comprehensive assessment of the state of *A. alba* of the artificial origin and its adult progeny, growing in rich soil conditions mixed with the main forest-forming species of the Forest in its Polish part. The results of the study can provide a basis for (1) a more substantiated approach to determining the potential range of silver fir in the north-eastern part of Poland and (2) clarification of the list of species recommended for artificial reforestation in this region of Europe. Moreover, as part of the study, an attempt to extract biometric parameters of trees based on terrestrial laser scanning (TLS) data was made.

MATERIAL AND METHODS

Location and characteristics of the material of the study

The material of this study, conducted in 2019 and 2020, was 30 silver fir trees (this is all that remains of an experience that began one century ago). Most of them were represented by old (mother) trees (18 pcs.) and other trees (12 pcs.) were the adult progeny of old firs (Fig. 1). These 12 trees were no longer located in the undergrowth and were also clearly not maternal trees. The present work focused on the study of the mother trees. In 1995, the 1.8-hectare site was fenced, where grew the old silver fir trees and their natural regeneration of different ages (Fig. 1), as well as the living and dead other tree species (Fig. 2).

Figure 1. The scheme of the placement of groups and trees of silver fir (modification of the drawing by M. Skowroński).

The trees were located in Białowieża Forest District, subcompartment 498 Ci. The GPS coordinates of

the centre of the site was E 23°48'53.2'', N 52°40'35.3'' (Fig. 3).

Figure 2. The number of living and dead trees by species.

The type of forest was LMśw – fresh, mixed broad-leaved forest, and the soil was rusty brown, not degraded. According to EFTC (European Forest Type

Classification 2006), based on the EUNIS (European Union Nature Information Scheme) forest classification, the type of forest can be classified as mesotrophic deciduous forests. The World Reference Base for Soil Resources (WRB) includes this soil in the Arenosols soil group (Bednarek and Prusinkiewicz 1997; IUSS Working Group 2014).

The following dates of planting (sowing) of the first studied appear in different publications: 1900–1910 (Korczyk 2008), 1928–1930 (Korczyk 1999) and 1928–1932 (Korczyk 1995). Thus, the age of the trees, according to the above data, can vary from 87 to 119 years. According to a description of the stand, the age of the trees is said to be 96 years (<http://www.bdl.lasy.gov.pl/porta1>). The unequal value of this important forestry indicator in different sources prompted us to conduct our own research.

No information was found on the initial characteristics of the forest cultural area – planting (sowing of seeds) under the canopy of an old forest stand, at the opening of the old stand without shelterwood, in a pioneer crop, under the canopy of naturally renewed

Figure 3. Location of Białowieża Forest and sample plot.

pioneer breeds, or in cutting. Unfortunately, the documentation was most likely lost without a trace during World War II. Lack of this important information also prompted us to try to reconstruct the conditions under which these trees appeared.

It should be noted that at the time of the study, no forest stand existed in the forestry sense of the word on the fenced surface. Initially, it was a mixed (group placement) forest stand of different ages. In addition to silver fir, in its composition were also Norway spruce (main breed), Scotch pine, common oak and common birch (admixtures). However, by the time of the study, already at the age of maturity of the forest, it had almost completely disintegrated. The main reason was the massive drying of Norway spruce that is characteristic of the Forest as a whole. There was drying out of pine and oak (Fig. 2). Many dead trees lay on the ground while most of them were still standing.

The silver fir and hornbeam (*Carpinus betulus* L.) were represented most in the undergrowth, also found was Norway spruce (*Picea abies* (L.) Karst), Scots pine (*Pinus sylvestris* L.) and common oak (*Quercus robur* L.). The under-forest was formed by European mountain ash (*Sorbus aucuparia* L.), European hazel (*Corylus avellana* L.), red elder (*Sambucus racemosa* L.), raspberry (*Rubus idaeus* L.) and dewberry (*R. caesius* L.). The living ground cover was composed of small nettle (*Urtica dioica* L.), bracken fern (*Pteridium aquilinum* (L.) KUHN), male fern (*Dryopteris filix-mas* L.) Schott), common speedwell (*Veronica officinalis* L.), wild strawberry (*Fragaria vesca* L.), sweet woodruff (*Asperula odorata* L.), yellow archangel (*Galeobdolon luteum* L.) and common hepatica (*Hepatica nobilis* Mill.). Other species were also present, but only sporadically.

Determining the age of old trees

The age of old trees (as of 2020) was determined using several methods, including non-standard ones:

1. The combined method (a): It is based on the calculation of the number of annual growths (annual rings) from different trees. Used: (1) calculation of the number of annual growths on the core taken in 2019 at a height of 1.3 m from a living tree (No. 18) and (2) calculation of the number of annual rings on the cuts made at the root neck and at a height of 1.3 m from a tree (No. 6/4) felled by a storm.
2. The combined method (b): It is based on the calculation of the number of annual rings on a cut made on the root neck of a tree (No. 6/4), felled by a storm, with an addition to the obtained value (75 years) of another 25 years since the beginning of the construction of the fence in 1995. Why? The top of the Norway spruce lying on the silver fir (No. 6/4), which interfered with the work, was then cut off. Consequently, it can be assumed that a storm pulled down the silver fir earlier than the Norway spruce and therefore, before 1995.
3. It is a method based on comparing the average values of the height and diameter of our stand with standard tabular data (Szymkiewicz 2001).

Assessment of the quality condition of trees

The study of the state of silver fir was carried out on the basis of a comparative analysis, by way of matching it with the wood species with which it grew. We studied the dynamics of the radial growth of silver fir and spruce over the past quarter-century. For this, the annual growth images scanned with a resolution of 600 dpi were analysed in the QGIS Software (Kotsan and Sevko 2019).

For assessing tree vitality, relative crown length, growth trends, crown deformation and trunk quality, the modified IUFRO scale was used (Jaworski and Paluch 2007).

Determination of stand characteristics

In this study, we used standard techniques usually practised in forestry. To determine the age, we calculated the number of tree rings on the core taken with the help of the incremental drill of Pressler from tree No. 18 (Fig. 1). But non-standard techniques were also applied.

The dbh (1.3 m) was measured with a calliper, as the height – using a SUUNTO PM-5/1520 height metre. The diameter data were distributed not by 4 cm thickness steps, as it is usually accepted, but by 5 cm ones, similar to the study by Korczyk (1999). This was done with the aim of a more objective comparative analysis of changes in this indicator, as well as the height and number of trees for more than 20 years.

The volume of trees of spruce, pine, oak, hornbeam and birch was determined approximately using the Denzin formula:

$$V = \frac{d^2}{1000} \cdot [1 + 0.03 (h - 30)]$$

where:

V – tree volume (m^3),

d – dbh (cm),

h – tree height (m) (Poschenrieder et al. 2016).

The dendrometric formula was used for a more accurate determination of the volume of silver fir trees:

$$V = g_{1.3} \cdot h \cdot f_{1.3}$$

where:

V – the volume of the tree (m^3),

$g_{1.3}$ – the basal area at the height of 1.3 m (m^2),

h – the height of the tree (m),

$f_{1.3}$ – form factor, taken from tables of Szymkiewicz (2001).

Terrestrial laser scanning data processing

As part of the study, an attempt to extract biometric parameters of trees based on terrestrial laser scanning (TLS) data was made. During the field campaign, a selected group of trees consisting of five firs (group No. 3 in Fig. 1) was scanned using a terrestrial laser scanner – Trimble TX5. The TLS data were collected by using the multi-scan approach (Liang et al. 2016): 1 central position (in the centre of the selected group of trees) and 6 positions outside the group of trees (Fig. 4). Four artificial targets (spheres) were used in order to merge scans performed from multiple positions.

The process of scans co-registration and point cloud exporting was conducted in the FARO Scene software (FARO Technologies, Inc., USA). In the next stage, the co-registered point cloud was divided into individual trees in the CloudCompare software (Girardeau-Montaut 2020). The individual trees extraction was done manually in order to separate the intersecting crowns as accurately as possible, and thus, the

Figure 4. A – crown ranges and the location of individual tree trunks on the sample plot (top view); B – scanned group of trees (side view).

points belonging to particular trunks and crowns of trees were selected.

Based on the preprocessed TLS data, the following dendrometric parameters of the trees were determined: tree height (TLS_H), dbh (TLS_DBH), basal area (TLS_BA), crown base height (TLS_CBH), crown projection area (TLS_CA), crown share (TLS_CS), crown volume (TLS_CVOL) and stem volume (TLS_VOL). The tree height was determined as the height of the highest registered point located within the crown of the particular tree. The height of the crown base was measured manually by the operator in CloudCompare software as the height measured to the first live branch of the crown of the tree. The dbh measurement was performed using an automatic RANSAC cylinder fitting algorithm (de Conto et al. 2017). Into a 10-centimetre slice of point cloud representing the tree trunk at a height of

1.25–1.35 m, a cylinder was automatically fitted, so as to it was possible to read the radius. The basal area has been calculated as the area of the cylinder base.

To calculate the stem volume, a method of building a three-dimensional trunk model was applied. Using the RANSAC cylinder fitting algorithm, a model consisting of a series of cylinders was created. Based on the generated model, it was possible to determine the total volume of cylinders, which was treated as the stem volume. It should be noted, however, that TLS technology has some limitations, and usually, it is not possible to rebuild the taper curve of the entire trunk, for example, due to the occlusion effect caused by mutual covering of branches in the upper parts of the tree crowns and by other neighbouring crowns (Wang et al. 2019). In order to minimize the underestimation of the stem volume caused by the inability to reproduce the entire taper curve, the authors

Figure 5. A – scheme of stem reconstruction (tree No. 5); B –crown shape reproduction (tree No. 1).

used the diameter of the last visible section of the trunk and the height of the highest registered crown point to create a cone – a simplified model of the unregistered part of the trunk was generated (Fig. 5).

To determine the volume of the crown, points previously classified as the tree crown were used using the Convex Hull algorithm (Fig. 5). This process was performed in MeshLab software (Cignoni et al. 2008). The created shape presents a generalized three-dimensional crown envelope. The crown area and coverage was determined based on the projection of the crown contours using GIS tools. The crown share was calculated as a percentage of the crown area that is shared with neighbouring crowns. In addition, based on TLS data, a visual assessment of the crown apex shape was made to evaluate the development phase of a given tree and its potential for growth. In this case, the assessment scale provided by Jaworski and Paluch (2007) was used.

Finally, the results of TLS measurements were compared with the ground measurements performed by traditional methods.

RESULTS

Age

1. The combined method (a): The number of annual growths on the core taken at the breast-height of a living tree (No. 18) was 86. The number of annual rings on the cut of a tree felled by a storm (No. 6/4) taken from the root neck was 75, and at a height of 1.3 m, it was 64. This means that in about 11 years, it took a young fir tree (No. 6/4) to reach a height of 1.3 m. Summing up $86 + 11 + 1$ (2019–2020), we estimated the age of tree No. 18 at the time of the study as at least 98 years old.

Despite the possibility of accurate ring calculation, this method cannot be deemed as absolutely reliable. Sometimes, in extreme weather conditions, trees form not one ring per year, but several or none at all.

2. The combined method (b): Based on the calculations, the age of the fir tree (No. 6/4), felled by the storm, would be at least 100 years old in 2020.

Since the date when the tree was felled by the wind is known only tentatively, this method is also not absolutely accurate.

3. Comparative method: As shown below, the average diameter of old trees (18 pcs.) was 41.9 cm, and the average height was 27.6 m. In the places of permanent residence of silver fir of I bonitet, these parameters according to Szymkiewicz (2001) correspond to the diameter – 103 years, while in height – only 75 years. As can be seen, this method provides an ambiguous answer as to the age of the trees. The discrepancy between the height and diameter is explained, in our opinion, by the fact that in recent years, trees do not grow in mixed stands, but in small groups located in open spaces due to the death of spruce and continued expansion of the open spaces. This phenomenon, apparently, influenced the fact that their phenotype to a greater extent begins to correspond to the appearance of separate trees, rather than growing in the forest stand.

Thus, the old fir trees in 2020 are likely to be at least 100 years old. Therefore, the date of planting (sowing of seeds) is approximately 1920 and before, which differs from the dates mentioned by Korczyk (1995, 1999, 2008, <http://www.bdl.lasy.gov.pl/portal>).

Condition of the species, growing together with silver fir

In order to assess the condition of silver fir, a comparative analysis was carried out of some forestry parameters of tree species growing together with the silver fir.

The Norway spruce population was the most significant, but the individuals in the lower classes of the diameter to 15 cm (78%) (Fig. 6) prevailed. Most of the older spruce trees had dried out. There were only approximately 3% of trees with a diameter of 25.1–40 cm left.

The number of hornbeams was less than Norway spruce. The younger generation dominated in the classes of the diameter from 5.1 to 10 cm (88%). There were no individuals present with a diameter of more than 15 cm. At present, hornbeam is the most expansive species in the Forest (Brzezicki 2017). This is clearly visible in our case.

Single individuals of common birch were noted in steps from 40.1 to 50 cm. The admixture of this species was the smallest.

The predominant part of oak trees (50 pcs. or 75%) had a diameter not exceeding 35 cm. Only in single in-

Figure 6. The distribution on the classes of the diameter of species growing together with silver fir.

dividuals (3 pcs. or 5%) was the diameter in the range from 85.1 to 100 cm.

Scotch pine was most significantly represented in the range of 35.1–55.0 cm (42 pcs. or 79%). There were no individuals with a diameter of less than 20 cm. One tree survived with a diameter in the range of 90.1–95.0 cm.

An analysis of the diameter distribution (Fig. 6) showed that spruce, hornbeam and birch growing together with silver fir did not form a normal stand. The curves of the diameter distribution of pine and oak to a certain extent corresponded to this. But since the trees of these species dispersed throughout the site and there were few, they didn't constitute a stand density even close to the minimum necessary degree. Therefore, as normal stands, pine and oak were also not represented.

A wide range of tree species on the site, as well as characteristics of under-forest and living ground cover, indicated rich soil conditions corresponding to the ecological and biological needs of silver fir.

Spruce dominated on the plot as in the case of living trees (55% of the total number or 261 pcs.) and in the case of dead trees (91% or 240 pcs.) (Fig. 2 and 7). Judging by the vitality of the still-living trees of this species, among which many were weakened and greatly weakened, they are likely to die in the future. As for the oak, the second largest species (14%), 12 individuals or

5% of the total number of all trees were killed. Pine, the third highest number species (11%), was characterized by a similar state to the previous species, with 3% of dead trees. The least represented was birch (4%), of which only one tree was dead.

Figure 7. The share of living and dead trees by species.

As can be seen, the main forest-forming species for the Białowieża Forest represented on the plot were spruce, oak, pine and birch, although to varying degrees; these trees are vulnerable, however, to dying due to abiotic and biotic factors. No dead hornbeam trees, of which the number was 9% of the total, were found (Fig. 7). Judging by the abundance of the hornbeam undergrowth (Fig. 6), in the future, this species will increase significantly. The situation of the plot described above is a peculiar snapshot, which on the whole objectively reflects the current state of these species in Białowieża Forest.

Comparing the vitality of silver fir and other species, this does not raise concerns yet (Fig. 2 and 7): the number of healthy trees was 30% or 94%, only two trees were dead. Moreover, these two trees weren't affected by a prolonged drought that weakened them, or by a subsequent attack of the bark beetle-typographer, as in the case of spruce. The reason, we believe, was as follows: a very tall silver fir tree (No. 6/4, 75 years old, and with a height of 31 m), and therefore unsustainable, was felled by the wind and, when it collapsed, broke the nearby tree (No. 6/3), which subsequently died.

As shown above (Fig. 2, 6 and 7), spruce, despite massive drying, still quantitatively continued to be the dominant species on the site. As well as silver fir, it is a dark coniferous species. It has similar requirements for soil and lighting conditions, and also a close rate of increase. The most significant difference is in the type of root systems: silver fir has a tap root system, with

4–5 powerful lateral roots directed down vertically, while Norway spruce has a pronounced superficial root system (Jaworski 2011).

Crucial for the understanding of the current state of these two species and future predictions is a retrospective assessment of the features of their growth. It was obtained based on an analysis of the annual radial increments. To minimize potential damage, cores were taken from only one old silver fir tree of a medium size (No. 18, see Fig. 1) and one Norway spruce (they both had approximately the same diameter and age). And only this circumstance explains the uncertainty of the data necessary for a full-fledged statistical analysis. Nevertheless, the available material made it possible to conduct a preliminary comparative analysis of tree-ring chronologies shown in the form of absolute radial increments (Fig. 8).

Of particular interest is the period preceding the beginning of the last mass drying of Norway spruce in Białowieża Forest in 2012 (Brzeziecki et al. 2018a), and further, up to the present. In 1994 was recorded a fairly significant synchronous decrease in the analysed parameter in both species. However, over the past quarter-century with its steadily warming trend, the dynamics of changes in the radial increment in these two species, as can be clearly seen from Fig. 8), were diametrically different. So, for example, the amplitude of the radial increment of silver fir varied from 0.14 to 0.32 cm.

While in Norway spruce, it was an order of magnitude less – only from 0.04 to 0.16 cm. These facts confirmed our assumption stated above that the remaining Norway spruce trees, most of which are currently weakened and severely weakened, are likely to die in the future.

Qualitative and quantitative parameters of trees

The state of mother trees with a division into separate positions, according to quality indicators, is presented in Table 1.

Table 1. Qualitative characteristics of mother trees

Indicator	Assessment		
	accepted in this classification, maximal		the investigated trees
	positive	negative	
Vitality	1	5	2.08
Relative length of the crown	1	4	1.83
Trend of growth	1	5	2.61
Deformation of crown	1	4	2.11
Quality of trunk	1	4	1.89

Analysing the obtained data, we can conclude that the qualitative characteristics of the mother trees corre-

Figure 8. The tree-ring chronologies of silver fir and Norway spruce.

spond to their age, and in most cases, the assessment of indicators is closer to the positive maximum.

The relatively good condition of the trees led to the stability of their number, supported by documentation. As follows from a comparison of the data of Korczyk (1999) and our own comparison, in more than 20 years,

only two trees have died due to the mechanical damage incurred as shown above. Unfortunately, we did not have data on the initial number of trees on the site and on the subsequent change in their number up to the time of the study.

Table 2. Parameters of mother trees and their adult progeny

Numbers and symbols of trees	The middle of the class of diameter [cm]	The height [m]	Form factor $f_{1,3}$	The basal area of the tree at a height of 1.3 [m ²]	The volume of the trunk [m ³]
Mother trees					
1	62.5	33	0.54	0.307	5.46
3	42.5	28	0.55	0.142	2.18
4	27.5	26	0.58	0.059	0.90
5	32.5	26	0.58	0.083	1.25
6	57.5	29	0.55	0.260	4.14
8	37.5	27	0.56	0.110	1.67
9	32.5	23	0.59	0.083	1.13
11	57.5	30	0.55	0.260	4.28
12	42.5	28	0.55	0.142	2.18
13	37.5	27	0.56	0.110	1.67
14	47.5	26	0.58	0.177	2.67
15	32.5	26	0.58	0.083	1.25
16	47.5	31	0.55	0.177	3.02
18	32.5	26	0.58	0.083	1.25
19	52.5	33	0.54	0.216	3.86
20	42.5	27	0.56	0.142	2.14
A	42.5	27	0.56	0.142	2.14
F	27.5	24	0.59	0.059	0.84
Adult progeny					
2	22.5	22	0.61	0.040	0.53
10	22.5	22	0.61	0.040	0.53
17	27.5	20	0.62	0.059	0.74
B	17.5	18	0.63	0.024	0.27
C	12.5	14	0.7	0.012	0.12
D	17.5	16	0.65	0.024	0.25
E	12.5	9	0.77	0.012	0.09
G	12.5	8	0.8	0.012	0.08
H	12.5	7	0.94	0.012	0.08
I	12.5	9	0.77	0.012	0.09
J	12.5	8	0.8	0.012	0.08
K	7.5	4	0.97	0.004	0.53

The expressed positive temporal dynamics of the height and diameter of silver fir trees should also be clearly noted. If, more than 20 years ago, the height of the tallest tree was 25 m, then in 2019 it was already 33 m. The diameter of the thickest tree was in the class of diameter of 35.1–40.0 cm, and it had moved to the class of 60.1–65.0 cm at the time of the study (Fig. 9).

Figure 9. Dynamics of changes in diameter and height.

In carrying out the total enumeration of trees, their main parameters and average statistical indices were determined (Tab. 2 and 3). As can be seen, by the size of the diameter, old trees were distributed over a wide enough class of diameter – from 25.1 to 65.0 cm. More than half of the trees (55%) were concentrated in the class from 30.1 to 45.0 cm. The lower class 25.1–30.0 cm was represented by two trees, and in the higher class from 50.1 to 65.0, four individuals were recorded (No. 1, 6, 11 and 19). They had the most significant height (from 29 to 33 m) and the volume of the trunk (from 3.86 to 5.46 m³).

The variability of the diameter and height was characterized by variation coefficients of 25.2% and 9.9%. The coefficient of variation of the volume of the trunks was 56.8%.

Individual No. 1 (Fig. 1), in our opinion, can be considered a candidate for advantage trees. Possessing the highest taxation indices (Tab. 2, Fig. 5B), at an age of about 100 years, it continued to abundantly bear fruit.

The number of adult progeny of old firs was extremely small – only 12 pcs. (6% of the total species stock in m³) per 18 mother trees, which strongly discredits with abundantly represented young natural regeneration this species up to 0.5 m high on the plot now. We believe that this situation indicates the digression of this category of offspring in the present and the even possible elimination of *A. alba* in the future. At the same time, we note that none of the trees of the adult progeny of old firs had signs of weakening under the influence of biotic or abiotic factors. Exactly half of them were represented in the 10–15 cm class (Tab. 2). The diameter floor was in the class of a diameter of 5–10 cm, and the upper one was in 25–30 cm. The coefficient of variation of diameters (36.5%) was much larger than that of the mother trees, but this, in principle, corresponds to the characteristics of young trees. The coefficient of variation in height was even more significant (48.6%). The amplitude of its variation was from 4 to 22 m (Tab. 3). This fact, in our opinion, indicates the diversity of the age of the preserved adult seed offspring.

Table 3. Statistical indicators of mother trees and their adult progeny

Indicator	d (cm)		h (m)		V (m ³)	
	*	**	*	**	*	**
Groups of trees						
Average value	41.94	15.83	27.61	13.08	2.34	0.24
Minimum	27.5	7.5	23	4	0.84	0.02
Maximum	62.5	27.5	33	22	5.46	0.74
Dispersion	111.44	33.33	7.43	40.45	1.77	0.06
Standard deviation	10.56	5.77	2.73	6.36	1.33	0.24
The coefficient of variation (%)	25.18	36.45	9.89	48.62	56.84	100

Note: * mother trees, ** adult progeny.

TLS-based measurements

An analysis of the biometric tree parameters estimated using the TLS data showed that the difference in the results of determining the most important tree traits (H, DBH, V) between the traditional method (field measurements) and TLS data is not significant (Tab. 2 and 4). The TLS-estimated tree height and stem volume are underestimated compared to field measurements. On the other hand, the DBH values obtained from the TLS

Table 4. TLS-based tree parameters

Tree No.	Stem parameters				Crown parameters				
	TLS_H [m]	TLS_DBH [m]	TLS_BA [m ²]	TLS_VOL [m ³]	TLS_CBH [m]	TLS_CL [m]	TLS_CA [m ²]	TLS_CVOL [m ³]	TLS_CS [%]
1	33.70	0.65	0.33	5.06	6.24	27.46	63.11	1546	22.33
2	23.49	0.24	0.05	0.76	9.89	13.60	19.23	274	72.06
3	27.41	0.46	0.17	2.54	6.86	20.55	38.30	830	34.32
4	24.21	0.31	0.08	0.98	6.99	17.22	32.19	512	30.74
5	22.40	0.33	0.08	0.97	6.37	16.03	34.32	452	10.55

data are higher than the reference values collected in the field.

The application of the TLS technology allowed to objective and precise estimation of tree crown metrics. The field measurements of these parameters were not performed due to the high time consumption and difficulties in the acquisition process, and in this connection, at the initial stage of the study, we limited ourselves only to a visual assessment (Tab. 1). The length of crowns for all five trees ranges from 58% to 81.5% of their relative height, which corresponds to grades 1 and 2 (Jaworski and Paluch 2007). Moreover, the maximum crown length ratio (81.5%) was observed for the most powerful tree (No. 1), which is even slightly more than $\frac{3}{4}$ of its height. The average distance between the trees in the group No. 3 is ca. 5 m, and the total horizontal projection of the crowns is about 190 m². Moreover, approximately 35% of this area is overlapped by projections of crowns of adjacent trees.

It has to be highlighted that significant percentage of overlap in the horizontal plane is created by well-developed crowns also in the vertical direction (Tab. 4). This, in particular, is indirectly evidenced by the fact of the complexity of scanning the upper part of the trunks mentioned above (Fig. 5A). This is due to the frequent arrangement of branches and their dense needles. The shape of the crowns of the analysed trees resembles quite high (from 13 to 27 m) irregular, narrow pyramids pointed at the top or even cylinders (Fig. 4 and 5). At different vertical levels, they touch, overlap and thus fill with their volume quite a significant total space above the ground. It is located starting from about 6 m above its surface and to a height of 34 m. Moreover, it was observed that the contribu-

tion of individual trees to the formation of the total crown volume (sum of TLS_CVOL) is significantly different. The share of tree No. 1 accounts for almost half (42.8%) or 1546 m³, while the contribution of the other trees is much lower: from 7.6% to 23%. It is visible that the leader tree, which has most successfully realized itself in a life race lasting 100 years, due to its crown, currently has the most significant influence in this biogroup. This case confirms one of the main paradigms of forest growing, which says that the main forester activities should be aimed at creating comfortable conditions for leader trees. An analysis of the results obtained using TLS allowed us to reveal a fairly clear pattern that we have not previously encountered in the literature: a change in the stem volume positively correlates with a change in the volume of crowns. Or in our case: when the stem volume decreases by 2–6.7 times compared to the leader tree, the volume of their crowns decreases by 1.9–5.6 times (Tab. 4). For monitoring purposes, it is planned to repeat the scanning of the area in the next 5 years, so it will be possible to estimate the growth of trees and assess changes in this stand.

The described situation would be more revealing if the analysed isolated group of trees was a fragment of a stand that has a normal spatial structure over a fairly large area. That is, if it was surrounded by other silver fir trees or trees of other species. Nevertheless, even with this objectively far from fully representative example, it can be seen that in the conditions of the Białowieża Forest, *A. alba* can form a typical multi-level vertical structure of the mother canopy typical of its stands, which is certainly necessary for the normal development of shade-tolerant undergrowth. At present, it is completely open to lateral sunlight.

DISCUSSION

There are generally accepted canons of artificial afforestation, including for silver fir, which however does not exclude some of their variability to depend on the specific conditions. In our case, we are obviously dealing with an out of the ordinary situation: a tree species typical of the medium and small mountains of central and southern Europe (Vitasse et al. 2019) of unknown geographical origin (Mejnartowicz 1996; Korczyk et al. 1997; Korczyk 2015a) grows on a plain, far beyond its continuous range. The closest natural island habitat of silver fir (not including Tisovik) is located 120 km south in the Jata *A. alba* nature reserve in Poland (Korczyk 1999).

As is well known, the volume of the trunk of individual trees is one of the most important indicators in forestry. It is this indicator, as well as the number of trees per unit area, that mainly determines the biological productivity of each forest ecosystem, which, in turn, condition such important functions of its as, for example, carbon sequestration and climate protection.

The very small number of old trees that nature, people and time left for us to study does not allow us to determine the stand volume per hectare with sufficient accuracy. But we compared the volume of the trunk of individual trees in our case and in the most typical conditions for silver fir in a continuous range. We believe that this approach is quite acceptable, and most importantly it is very informative. As it turns out, the average volume of individual trees in the Carpathians was from 2.5 to 3.3 m³ (Dobrowolska et al. 2015), and this is essential lower than that established by our research (see above). This result clearly testifies to the high potential productivity of silver fir in Białowieża Forest.

Note that in our case, both the relative and absolute lengths of crowns (Tab. 1 and 4) were longer than those of old age silver fir in Beskidy Zachodnie (Jaworski and Paluch 2007). Both this fact and the disproportionality of the diameter and height (see the section “Age”) are not, in our opinion, genetically determined. The mother trees are surrounded only by dried Norway spruce trees still standing on their roots, the number of which decreased after each strong wind episode. The above morphological features were formed gradually under the influence of increased illumination as a result of the decay of the Norway spruce part of the stand, as a varia-

tion of the phenotype within the modification variability of the species.

In this regard, a comparison of the parameters of the studied trees and those in the Beskid Niski (continuous range) is very indicative. The average diameter and height of the mother trees in the Forest was 41.9 cm and 27.6 m, respectively (Tab. 3). In the Beskid Niski, trees with an age of more than 110 years have such a diameter and height the same as in the Forest – approximately 70-year-old individuals (Bruchwald et al. 2015). That is, the disproportion of the two most important stand characteristics, expressed using the age of trees growing in the most favourable conditions, is about 40 years. One more example leads us to a similar conclusion. In the typical Carpathian selection silver fir forests (Limanowa, Łosie II and Stary Sącz II), with about the same age as the studied trees, the diameter varies from 22.3 to 24.4 cm and the height in the range of 33.5–40.6 m (Jaworski et al. 2007).

At the same time, the coefficients of variation of the trees diameter and height in the Forest are close to similar indicators of these stands. The coefficient of variation of the volume of the trunk was approximately twice higher than the coefficient of variation of its diameter. It corresponds to the proportion between these indicators known in the forest mensuration of stands.

But there is an example of the interaction of one of the genotypes with environmental conditions, which led to the appearance of a phenotype different from the above. This tree (No. 6/4), unfortunately, was already lost. About 25 years ago, it was brought down by a storm (Fig. 1). The height of the tree at the age of 75 years was 31 m. The dbh was 0.53 m. We note in this regard that the oldest Białowieża silver fir from the Tisovik tract, felled by the wind in 1922, had a height of 33.5 m and was at least 250 years old (Srodoń 1983). The oldest silver fir from the Jata reserve, the closest island natural habitat of *A. alba* to Białowieża Forest, was 34 m high at the age of 205 years (Korczyk 1999). We believe that the studied tree reached such a considerable height due to its good genotype, but also due to the fact that, in contrast to the currently living silver firs, it grew in an authentic mixed forest stand. The Norway spruce – its main breed, which has not been exposed to negative abiotic and biotic factors a quarter-century ago and earlier, as well as the admixtures – Scots pine and common oak, competing with silver fir, stimulated

its growth in height and at the same time created the necessary density of crowns. This example confirms the conclusions of Dobrowolska et al. (2015) that with the corresponding phytocenotic structure of the stand in rich soil conditions, *A. alba* in Poland can reach very significant parameters outside the continuous range.

The flow of new individuals from the undergrowth to the upper storey determines the future of each species of tree. Without continuous replenishment of the upper storey, the species worsen its own position. In this regard, depending on its role in the forest stands, it can occur either as a change of leader, sometimes undesirable or the disappearance of a co-dominant species or of admixture. In order to be successful, each of the species must be constantly and in sufficient quantity represented by the following cenotic groups: seedlings, undergrowth (small, medium and large), individuals coming out into the lower storey of the stand (adult progeny of old trees) and the trees forming the upper storey. For silver fir stands, this condition is more fundamental than for other trees (Jaworski 2011).

It was shown that the number of adult progeny of old firs was represented in a very small amount and does not ensure continuity of *A. alba* generations. A similar situation occurs in other studies of the natural regeneration of silver fir outside its range (Dobrowolska et al. 2015). It is believed that its success in the lowlands of Poland is largely determined by the species composition of the forest stand (Dobrowolska 1998). We recalled that in our case, the stand had actually been falling apart. In this regard, the problem may lie in the fact of the mismatch of lighting conditions. As was shown, the hornbeam undergrowth was abundantly represented on the site. Currently, it is the most expansive species in Białowieża Forest that limits the natural regeneration of key species (Brzeziecki et al. 2018b). Probably, in this case, due to its higher expansion, it limits the number of the young generation of silver fir. Herbivorous animals have a negative effect on seedlings and undergrowth (Vitasse et al. 2019). But, since the site was fenced, the influence of this factor, starting in 1995, can be excluded. In addition, trees lying on the ground, mainly Norway spruce, represent a serious obstacle for animals. Our assumption about the different ages of the surviving adult progeny of old *A. alba* is confirmed in the literature. Korczyk (1999) wrote about the presence of at least two generations of silver fir on the site; but

more than 20 years have passed, and the situation has not changed. A generation up to 1 m and above (large undergrowth) preceding the adult progeny of old firs is represented by a single individual. The reasons for the insufficiently active quantitative implementation of the adult progeny of old firs into the canopy of the dominant trees still need to be clarified. This is puzzling, and the analysis of the natural renewal of silver fir in Tisovik by Korczyk et al. (1997) also didn't answer the question about the cause of the mass death of annual seedlings.

Since 1995 (Korczyk 1999), to the present day on the site, it has not been established that the loss of silver fir (maternal trees and their adult progeny) is due to climate change and the negative influence of the biotic factor, as is the case with Norway spruce. This fact, as well as the results of an analysis of the dynamics of the radial increment, including in the comparison with Norway spruce (Fig. 8), indicates a high degree of stability of *A. alba* trees at the time of the study.

As is known, this species is very demanding with regard to air humidity (Jaworski and Zarzycki 1983; Bernadzik 2008). However, there has been a decrease in this indicator in Europe in recent years (Vitasse et al. 2019). And regardless of this fact, in our opinion, thanks to a well-developed root system, the species provides itself with moisture, compensating in this way for the increased transpiration associated with the deficiency of moisture in the air. Moreover, perhaps, due to the noted morphology of the underground organs, it is even able to increase the stability of mixed stands by redistributing moisture from wetter soil horizons to drier ones (Töchterle 2020).

The thermal regime of the winter period has substantially changed in Białowieża Forest over the past 70 years. Winters have become milder and shorter, and the vegetation period has increased by 2 days every 10 years. The average daily temperature has increased by 0.3 °C per decade and is 7.7 °C now (Malzahn et al. 2014).

The results of our study, as well as climatic transformations, suggest that the eastern border of the silver fir's range, referred to in the literature as the border of frosty winters (Jaworski 2011), has changed its configuration. Obviously, Białowieża Forest can be included in the optimistic model of the potential range of *A. alba* (Bolibok et al. 2016). The basis for this is also the soil conditions. The old-glacial denuded moraine plateaus

with high-fertile brown soils, often with traces of gleyification, dominate in the Polish part of Forest (Kwiatkowski 1994, Prusinkiewicz and Michalczuk 1998). They are favourable for fir growth including through to their pronounced ability to absorb precipitation (Bernadzki 2008; Jaszcak et al. 2008; Jaworski 2011), which is very important in the context of general climate warming (Bolibok et al. 2016).

The TLS technology gives a chance to collect the tree parameters which are difficult or not possible to obtain by using the conventional tools. It should be noted, however, that the application of the TLS in forestry has some limitations related to technology itself (static method of measurement – point cloud is registered from selected positions) and the complex forest structure (due to the occlusion effect caused by mutual covering of branches in the upper parts of the tree crowns and by other neighbouring crowns). Added value of the TLS application is the ability to precise measurement of the crown metrics, which is extremely difficult or impossible to obtain by application of the traditional inventory methods. This aspect is extremely necessary for an objective assessment of the state of trees, as well as for characterizing the conditions for the growth and development of undergrowth.

CONCLUSIONS

High forestry stand characteristics of old silver fir (diameter, height, volume of a tree and crown) provide an objective concept of their successful growth process. All these facts can be interpreted as evidence of the correspondence of local soil-hydrological and microclimatic conditions to the constitution of the studied *A. alba* population. High growth rates of silver fir have been established in fresh, mixed broad-leaved forest, and this fact must be taken into account when carrying out artificial reforestation.

In the group of trees of the adult progeny of old firs, no individuals had been identified as weakened under the influence of negative factors. The growth parameters are acceptable and correspond to cenotic status. However, their disproportionately small number indicates some kind of malfunction in the mechanism of natural generational change, requiring detailed studies.

The results of this study do not give grounds for rejecting the hypothesis that European silver fir could be an alternative to drying Norway spruce in Białowieża Forest. This suggests that it can be included in the potential range of this species.

The obtained results showed a great potential of the TLS technology in the silviculture studies. The TLS-based measurements do not differ significantly from the reference measurements.

REFERENCES

- Bednarek, R., Prusinkiewicz, Z. 1997. Geografia gleb (in Polish). PWN, Warszawa, Poland.
- Bernadzki, E. 2008. Jodła pospolita. Ekologia – zagrożenia – hodowla (in Polish). PWRiL, Warszawa, Poland.
- Bolibok, L., Zajączkowski, J., Dobrowolska, D., Mionskowski, M. 2016. Potential climatic range for *Abies alba* Mill. in Poland (in Polish with English summary). *Sylvan*, 160 (6), 519–528.
- Bruchwald, A., Dmyterko, E., Niemczyk, M., Łukasiewicz, J. 2015. Height and diameter growth rates of silver fir (*Abies alba* Mill.) growing in Beskid Niski mountains (in Polish with English summary). *Sylvan*, 159 (10), 804–812. DOI: 10.26202/sylvan.2015003
- Brzezicki, B. 2017. Wieloletnia dynamika drzew i drzewostanów Rezerwatu Ścisłego Białowieskiego Parku Narodowego (in Polish). In: Lasy Rezerwatu Ścisłego Białowieskiego Parku Narodowego (eds. T. Borecki et al.), Białowieża, Poland, 94–125.
- Brzezicki, B. et al. 2018a. Problem of a massive dying-off of Norway spruce stands in the ‘Białowieża Forest’ Forest Promotional Complex (in Polish with English summary). *Sylvan*, 162 (5), 373–386. DOI: 10.26202/sylvan.2017129
- Brzezicki, B., Andrzejczyk, T., Żybura, H. 2018b. Natural regeneration of trees in the Białowieża Forest (in Polish with English summary). *Sylvan*, 162 (11), 883–896. DOI: 10.26202/sylvan.2018116
- Cignoni, P., Callieri, M., Corsini, M., Dellepiane, M., Ganovelli, F., Ranzuglia, G. 2008. MeshLab: an Open-Source Mesh Processing Tool, Sixth Eurographics Italian Chapter Conference, 129–136.

- de Conto, T., Olofsson, K., Görgens, E.B., Rodriguez, L.C.E., Almeida, G. 2017. Performance of stem denoising and stem modelling algorithms on single tree point clouds from terrestrial laser scanning. *Computers and Electronics in Agriculture*, 143, 165–176. DOI: 10.1016/j.compag.2017.10.019
- Dąbrowski, M.J. 1959. Late-glacial and Holocene history of Białowieża Primeforest Part I. Białowieża National Park (in Polish with English summary). *Acta Societatis Botanicorum Poloniae*, 28 (2), 197–248.
- Dobrowolska, D. 1998. Structure of silver fir (*Abies alba* Mill.) natural regeneration in the ‘Jata’ reserve in Poland. *Forest Ecology and Management*, 110 (1/3), 237–247. DOI: 10.1016/S0378-1127(98)00286-2
- Dobrowolska, D., Olszowska, G., Pawlak, P. 2015. Weryfikacja istniejących zasięgów występowania głównych lasotwórczych gatunków drzew w Polsce na podstawie nowych badań. Jodła pospolita (*Abies alba* Mill.) w badaniach hodowlanych na terenie Polski (in Polish). BLP–358, appendix No. 27. Available at https://tbr.lasy.gov.pl/apex/f?p=102:3:::NO::P3_TEMAT:3483 (access on 12 May 2020).
- European Forest Type Classification. 2006. European Environment Agency. Technical report 9. Copenhagen.
- Girardeau-Montaut, D. 2020. CloudCompare – 3D Point Cloud and Mesh Processing Software (Version 2.11). GPL Softw. Available at <http://www.cloudcompare.org/> (access on 1 May 2020).
- IUSS Working Group. 2014. World reference base for soil resources 2014. International soil classification system for naming soils and creating legends for soil maps. FAO, Rome, Italy. Available at <http://www.fao.org/publications/card/en/c/942e424c-85a9-411d-a739-22d5f8b6cc41/> (access on 12 May 2020).
- Jaszcak, R., Magnuski, K., Małys, L. 2008. European silver fir (*Abies alba* Mill.) growing in conditions of clear cutting as well as shelter wood and group cutting after cleaning cutting of hornbeam-oak old forest. *Acta Scientiarum Polonorum. Silvarum Colendarum Ratio et Industria Lignaria*, 7 (3), 15–22.
- Jaworski, A., Zarzycki, K. 1983. Ekologia (in Polish). In: Nasze drzewa leśne. Monografie Popularnonaukowe, T. 4. Jodła pospolita *Abies alba* Mill. (ed.: S. Białobok), PWN, Warszawa–Poznań, 317–430.
- Jaworski, A., Paluch, J. 2007. Charakterystyka cech morfologicznych jodeł w drzewostanach o strukturze przerębowej Beskidów. *Leśne Prace Badawcze*, 3, 7–31.
- Jaworski, A., Paluch, J., Pach, M., Kołodziej, Z., Majerczyk, K. 2007. Characteristics of selection stands in selected forest districts of the Cracow Regional Directorate of State Forests (in Polish with English summary). *Sylvan*, 151 (6), 34–52.
- Jaworski, A. 2011. Hodowla lasu. Charakterystyka hodowlana drzew i krzewów leśnych (in Polish). PWRiL, Warszawa, Poland, T. III.
- Korczyk, A. 1995. Protection and conservation of gene resources of forest trees in the Białowieża Forest (in Polish). In: Protection of forest ecosystems biodiversity of Białowieża primeval forest. (eds.: S. Zajączkowski et al.), SGGW, Warszawa, Poland, 95–102.
- Korczyk, A., Kawecka, A., Martysevič, V., Strelkov, A. 1997. Naturalne stanowisko jodły pospolitej (*Abies alba* Mill.) w Puszczy Białowieskiej (in Polish). *Prace Instytutu Badawczego Leśnictwa*, 837, 27–62.
- Korczyk, A.F. 1999. Ocena wartości genetycznej i hodowlanej naturalnych populacji jodły pospolitej (*Abies alba* Mill.) ze wschodniego zasięgu w Polsce (in Polish). *Zeszyty Naukowe Akademii Rolniczej im. H. Kołłątaja w Krakowie*, 339, 155–170.
- Korczyk, A.F. 2008. Inwentaryzacja drzew starych i drzew gatunków ginących w Puszczy Białowieskiej. *Leśne Prace Badawcze*, 69 (2), 117–126.
- Korczyk, A. 2015a. The ‘Tisovik’ reserve of Silver fir in the Belarusian national park ‘Belavezhskaya Pushcha’. *Leśne Prace Badawcze*, 76 (1), 18–36. DOI:10.1515/frp-2015-0002
- Kotsan, V., Sevko, O. 2019. Dynamika radialnego przyrostu sosnowych drzewostanów o różnej strukturze i warunkami przebiegu (in Russian). *Trudy BGTU, Ser. I*, 2(222), 16–19.
- Kwiatkowski, W. 1994. Krajobrazy roślinne Puszczy Białowieskiej (in Polish). *Phytocoenosis. Supplementum Cartographiae Geobotanicae*, 6 (6), 35–87.
- Liang, X., Kankare, V., Hyypä, J., Wang, Y., Kukko, A., Haggrén, H. et al. 2016. Terrestrial laser scanning in forest inventories. *Journal of Photogrammetry and Remote Sensing*, 115, 63–77. DOI: 10.1016/j.isprsjprs.2016.01.006

- Litkowiec, M., Lewandowski, A. 2015. Postglacial history of silver fir (*Abies alba* Mill.) in Poland as a result of migration from different refugia – the current state of knowledge (in Polish with English summary). *Sylwan*, 159 (2), 109–116. DOI: 10.26202/sylwan.2014123
- Malzahn, E., Pierzgalski, E., Tyszką, J., Janek, M., Fronczak, E., Stolarek, A. 2014. Zmiany warunków klimatycznych i wodnych w środowisku lasów naturalnych Puszczy Białowieskiej (in Polish). BLP–361. Available at <https://tbr.lasy.gov.pl/apex/f?p=102:2:::NO>
- Mejnartowicz, L. 1996. Origin of Silver-fir stands in Białowieża Primeval Forest. In: Biodiversity Protection of Białowieża Primeval Forest. (eds.: P. Paschalis, S. Zajączkowski), Fundacja Rozwój SGGH, Warszawa, Poland, 35–50.
- Neuner, S., Albrecht, A., Cullmann, D., Engels, F., Griess, V.C., Hahn, W.A., et al. 2015. Survival of Norway spruce remains higher in mixed stands under a drier and warmer climate. *Global Change Biology*, 21 (2), 935–946. DOI: 10.1111/gcb.12751
- Paczoski, J. 1930. Lasy Białowieży (in Polish). Państwowa rada ochrony przyrody, Poznań, Poland.
- Pomortsev, O.A., Kashkarov, E.P., Lovelius, N.V. 2015. Bioklimatičeskaja chronologija golocena: rekonstrukcijz i prognoz (in Russian). *Vestnik of the north-eastern federal university named after M.K. Ammosov*, 3 (47), 100–115.
- Poschenrieder, W., Rais, A., van de Kuilen, J.-W.G., Pretzsch, H. 2016. Modelling sawn timber volume and strength development at the individual tree level – essential model features by the example of Douglas fir. *Silva Fennica*, 50 (1), 25. DOI: 10.14214/sf.1393
- Prusinkiewicz, Z., Michalczyk, C. 1998. Gleby Białowieskiego Parku Narodowego. Historia badań, środowisko glebotwórcze, geneza i systematyka oraz przestrzenna zmienność gleb (in Polish). *Phytocoenosis*, 10 (10), 29–40.
- Srodoń, A. 1983. Jodła pospolita w historii naszych lasów (in Polish). In: Nasze drzewa leśne. Jodła pospolita *Abies alba* Mill. (ed.: S. Białobok), PWN, Warszawa–Poznań, T. 4, 9–39.
- Szafer, W. 1920. Jodła w Puszczy Białowieskiej (in Polish). *Sylwan*, 38, 103–112.
- Szymkiewicz, B. 2001. Tablice zasobności i przyrostu drzewostanów ważniejszych gatunków drzew leśnych (in Polish). PWRiL, Warszawa, Poland.
- Töchterle, P., Yang, F., Rehschuh, S. et al. 2020. Hydraulic Water Redistribution by Silver Fir (*Abies alba* Mill.) Occurring under Severe Soil Drought. *Forests*, 11 (2), 162. DOI: 10.3390/f11020162
- Vitasse, Y., Bottero, A., Rebetez, M., Conedera, M., Augustin, S., Brang, P. et al. 2019. What is the potential of silver fir to thrive under warmer and drier climate? *European Journal of Forest Research*, 138 (4), 547–560. DOI: 10.1007/s10342-019-01192-4
- Wang, Y., Lehtomäki, M., Liang, X., et al. 2019. Is field-measured tree height as reliable as believed – A comparison study of tree height estimates from field measurement, airborne laser scanning and terrestrial laser scanning in a boreal forest. *Journal of Photogrammetry and Remote Sensing*, 147, 132–145. DOI: 10.1016/j.isprsjprs.2018.11.008
- Wick, L., Möhl, A. 2006. The mid-Holocene extinction of silver fir (*Abies alba*) in the Southern Alps: a consequence of forest fires? Palaeobotanical records and forest simulations. *Vegetation History and Archaeobotany*, 15, 435–444. DOI: 10.1007/s00334-006-0051-0