

The needle percentage in the leafy shoot biomass of Scots pine in climate gradients of Eurasia

Vladimir Andreevich Usoltsev^{1,2}, Walery Zukow^{3*}, Ivan Stepanovich Tsepordey²

¹Ural State Forest Engineering University, 620100 Yekaterinburg, Sibirskiy Trakt, 37, Russia

²Botanical Garden of Ural Branch of RAS, 620144 Yekaterinburg, str. 8 Marta, 202a, Russia

³Faculty of Earth Sciences and Spatial Management, Nicolaus Copernicus University, str. Lwowska 1, 87-100 Toruń, Poland

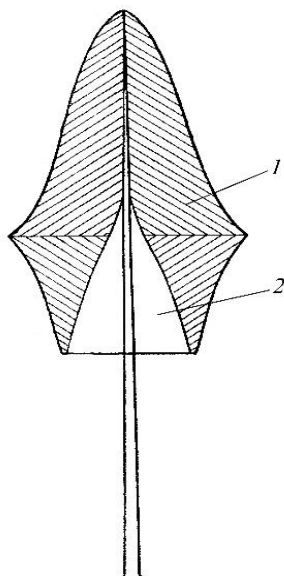
*corresponding author's e-mail: zukow@wp.pl

Abstract. The efficiency of using photosynthetically active radiation by trees largely depends on the architecture of the assimilation apparatus in their crown. It is known that an increase in the level of atmospheric pollution is accompanied, on the one hand, by an increase in the foliage density on the leafy shoot length, and on the other hand, by an increase in the transparency of the crown due to the expansion of the leafless inner part of the crown. On this basis, we assume that the foliage percentage of leafy shoots (*PL*) is a sensitive indicator of changes in growing conditions not only due to environmental pollution, but also in broader ecological aspects, in particular, in the geographical or climatic gradients of Eurasia. For this purpose, a database of empirical data has been formed in the amount of 558 model trees of Scots pine of natural and artificial origin from 6 regions of Northern Eurasia with a measured percentage of needle in the leafy shoot biomass. A regression model has been designed, in which the contributions of mensuration variables (tree age and stem diameter), climatic variables (temperature and precipitation) and the origin of stands (natural and artificial) to explain the variability of the desired *PL* indicator are 15, 53 and 30 %, respectively. It is concluded that with a decrease in annual precipitation from 600 to 300 mm, there is an increase in *PL* by 0.2..0.3% for every 10 mm of annual precipitation, both in natural stands and in plantations. When the January temperature decreases from 0°C to -20 °C, *PL* increases by 0.8..1.0% for each 1°C. Thus, the foliage percentage of leafy shoots of Scots pine is an indicator of changes in growing conditions in the climate gradients of Eurasia.

Keywords: needle percentage in the leafy shoot biomass, regression model, dendrometric indicators of trees, natural stands and plantations, averaged January temperature, averaged annual precipitation.

1. Introduction

The ability of forest trees to extract atmospheric carbon dioxide and produce organic matter is the basis of their functioning (Budyko, 1964; Dylis, 1978). The efficiency of using photosynthetically active radiation by tree crowns largely depends on the architecture of the assimilation apparatus associated with such concepts as the “volumetric density” of foliage biomass (Protopopov & Gorbatenko, 1967), or “phytosaturation” of foliage, as the foliage biomass divided by the crown space occupied by foliage (Usoltsev, 1985, 2013), or “density” of foliage biomass as dry weight of foliage divided by crown surface area (Mizoue & Masutani, 2003). The architecture



of the assimilation apparatus is also associated with such a concept as the crown transparency (Tsel'niker, 1969). It is defined as the ratio of the area of the crown gaps to the area of the entire crown on its frontal projection and varies from 0.05 in shade-tolerant Norway spruce to 0.32 in light-demanding Scots pine (Zel'niker, 1969). In light-demanding species, already in 10-20 age, the crown is divided into the mantle (Kronenmantel), or the leafy part of the crown, and the crown core (Kronenkern), or the leafless part of the crown along the stem axis (Fig. 1) (Burger, 1939; Assman, 1961).

Fig. 1. Scheme of crown division into the mantle (1) and the core (2) areas (modified after Burger, 1939)

The specificity of crown architecture consists in the subordination

of branches of different orders that ensure its mechanical stability, the ways of xylem and phloem transport and the balance of organic matter (Münch, 1938; McMahon & Kronauer, 1976; Valentine, 1988; Tsel'niker, 1995; Poorter et al., 2008; Ishii & Asano, 2009; Yagi, 2011; Iida et al., 2011; Echereme et al., 2015; Jucker et al., 2015; Yang et al., 2015; Pallas et al., 2016; Xu et al., 2019; Chen et al., 2022). As the tree grows, the volume of the crown increases, while in light-demanding species the proportion of the core in the crown increases, whereas in shade-tolerant species it changes slightly in relation to light-demanding ones (Rudnev, 1977).

So, tree architecture is related to the availability of radiation at a given position within a tree crown (Yang et al., 2015). In the gradient of decreasing illumination inside the crown, its mantle in light-demanding species is increasingly moving away from the stem axis with age and shifting to the periphery of the crown. At the same time, the leafless part expands not only along the stem, but also along the branches, first along the branches of the 1st order, then along the branches of the 2nd order, etc., i.e. the assimilation apparatus is increasingly concentrated in the surface part of the crown mantle, exclusively on the leafy shoots (Mayer, 1980). For example, in white birch trees aged 8, 18, 31 and 50 years, the proportion of leafy shoots in the crown biomass is 100, 67, 56 and 20%, respectively (Ilyushenko, 1970), i.e. over a 40-year period there is a 5-fold decrease in the proportion of leafy shoots in the crown biomass.

The number of branching orders in the crown is limited in forest trees to four or five (Tsel'niker, 1995; Avdeeva & Krivonosenko, 2013), and branches of the last order are usually represented by leafy shoots. The term "shoot" or "segment" in the literature has no single definition, and the discussion is mainly about its age and position in the crown (Serebryakov, 1952; Grudzinskaya, 1960; Nukhimovsky, 1974; Mazurenko & Khokhryakov, 1974; Ford et al., 1990; Room et al., 1994; Zel'niker et al., 2000; Serebryakova et al., 2006; Yagi, 2011; Sargent, 2013). In our presentation, the concept of "leafy shoot" is not related to age or position in the crown, it may include the axis increment of 1-2 years in the upper part of the crown and the increment of several years in the lower crown part. The main feature of the concept of "leafy shoot" is the presence of foliage along the entire length of its main axis and lateral (overgrown) branches.

There is a close relationship between the length of the shoot and the needle biomass on it (Sander & Eckstein, 1994; Tsel'niker, 1995). As a result, the proportion of assimilation mass in leafy shoots (crown greenery) is a fairly stable value, its coefficient of variation in pine, birch and aspen varies only from 2 to 5% (Gorbatenko, 1970; Usoltsev, 1985). The proportion of foliage in leafy shoot biomass is in larch 45 ± 3.5 % (Yablokov, 1934), in birch 63.4 ± 0.5 %, in aspen 70.0 ± 1.6 % (Usoltsev, 1973), in pine 78% (Ivanchikov et al., 1982).

It is known that with the deterioration of growing conditions, the share of the assimilation apparatus in the aboveground biomass increases. In the worst conditions, trees increase the mass of the most vital organ - the assimilation apparatus, thereby compensating for its reduced activity in these conditions (Smirnov, 1971; Usoltsev, 1974; Alekseev, 1975). A similar pattern is repeated in stressful conditions of stands subject to air pollution. In the conditions of air pollution, the growth of the apex and upper branches is most significantly reduced, which leads to a change in the architecture of the crown. It becomes flat-topped, and with more severe damage - dry-topped and resembles the crown of old-age trees in its shape (Yuknis, 1987; Yarmishko, 2009). As we approach the sources of air pollution, the share of foliage in the crown mass of pine (Yusupov et al., 1997), spruce and fir (Usoltsev et al., 2012), as well of birch (Zavyalov, 2009) increases.

In many coniferous species, an increase in the needle density on shoots has been found due to the advance from background areas to the source of air pollution (Augustaitis, 1989, 1992; Yarmishko, 1997; Zalesov & Bachurina, 2008; Zarubina, 2011) or with an increase in the content of heavy metals in tree needles (Tarkhanov, 2011). Sometimes, the increase in the level of air pollution is accompanied by an increase not only in the density of the needles, but also in their linear dimensions (Sidaravicius, 1987). At the same time, there is a decrease in the life expectancy (longevity) of needles (Yarmishko, 1989; Torloпова & Robakidze, 2003; Zalesov & Bachurina, 2008).

Strange as it may seem at the first glance, a decrease in the life expectancy of needles as the degree of air pollution increases, leads to an increase in the proportion of needles in the biomass of leafy shoots. Figure 2 shows a decrease in the life expectancy of Scots pine needles from 4 years (right) to 1 year (left) as they approach the source of pollution. It is obvious that as the life expectancy of needles decreases, the proportion of the leafless part of shoots increases, and there is a further expansion of the crown core. This expansion is initially due to the fall of the needles of the 4th year, then the needles of the 3rd year, etc. Since there is an inversely proportional relationship between the age of Scots pine needles in polluted conditions and the density of needles in the segment of the corresponding year (Zubareva, 1993), then as the needles of previous years fall off and the corresponding "rejuvenation" of the shoot, the proportion of needles in the biomass of the leafy shoot increases. Therefore, the proportion of needles in the biomass of the current year's shoot is always higher than the proportion of needles in a shoot bearing needles for several years. For example, according to K.S. Bobkova et al. (1986), the needle percentage in the leafy shoots of Scots pine varies from 64 to 77%, depending on the type of forest. But in the biomass of shoots of the current year, the proportion of needles of Scots pine is significantly higher (ranging from 80 to 83%) than the proportion of needles in the biomass of all leafy shoots (Bobkova et al., 1986) and varies slightly by forest types (Kamenetskaya, 1970).

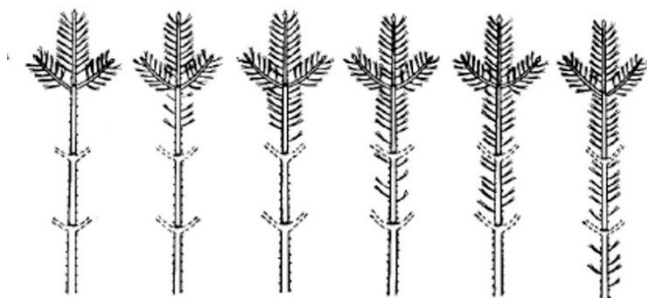


Fig. 2. Decrease in the longevity of needles from 4 years (right) to 1 year (left) as they approach the source of air pollution (Jäger, 1980; cited and modified according to: Schubert, 1985).

A similar pattern was shown on the shoots of *Abies alba* in the botanical gardens of Tharandt and Halle in Germany (Fig. 3). As a result of the fact that sulfur dioxide pollution in Halle is four times higher than in Tharandt, the longevity of needles in Halle is two years shorter. But the decrease in the density of needles in segments of different ages occurs much more intensively in Halle: from 100% in the segment of the current year to 10% in the segment that has grown 3 years ago, whereas in Tharandt the corresponding decrease is only from 100% to 80% (Schubert, 1985). In this case, it also becomes obvious that as the needles of previous years fall off, the proportion of needles in the leafy shoots naturally increases.

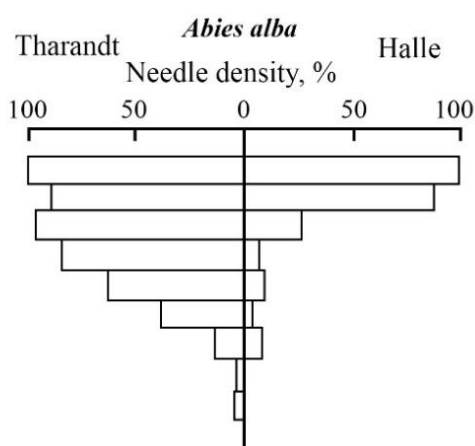


Fig. 3. Covering of annual segments (located from top to bottom) with needles (%) as an expression of the proportion of needles in segments of different years and longevity of *Abies alba* needles in the botanical gardens of Tharandt and Halle (modified after Schubert, 1985).

On the other hand, as we approach the source of air pollution, the transparency of tree crowns increases many times due to the intensive needle fall along the stem and branches of the 1st, 2nd, etc., orders and the corresponding expansion of the crown core (Sidaravicius, 1987; Yarmishko, 1990; Brassel & Schwyzer, 1992; Nizametdinov, 2009). Thus, as the degree of air pollution increases, the natural expansion of the crown core due to the lack of radiation inside crown becomes more intense due to pollution, and in some extreme cases, the crown mantle focuses on the shoots of the current year. Since we are talking here about

the proportion of needles in the leafy shoots, this proportion increases as we approach the source of pollution.

Apparently, an increase in the transparency of the crown due to the expansion of its leafless core and an increase in the needle density of the shoots on the periphery of the crown mantle are two components of a common process caused by the reaction of the tree to air pollution. Based on the above, we assume that the needle percentage of leafy shoot biomass is a sensitive indicator of changes in growing conditions not only due to environmental pollution, but also in broader ecological relations, in particular, in the climate gradients of Eurasia.

Since the 1930s, a simplified methodology has been used in the forests of Northern Eurasia (present-day Russia, Ukraine and Kazakhstan) to determine the biomass of foliage. According to this method, the leafy shoots of the entire crown were cut off with a pruner and weighed, while a sample of the resulting mass of shoots was taken to determine the share of foliage in leafy shoots and then the biomass of the foliage of the entire tree was calculated (Yablokov, 1934; Molchanov & Smirnov, 1967; Baizakov, 1969; Kamenetskaya, 1970; Usoltsev, 1985; Lakyda, 2002). These data on the foliage percentage in the leafy shoots were stored in the archives of researchers, and were recently brought together and published in the corresponding database (Usoltsev, 2020).

In the following presentation, the concept of a leafy shoot assumes the presence of needles along the entire length of the shoot. As far as we know, there is no data in the literature on geographical patterns of the foliage percentage in the leafy shoot biomass of tree crowns. It is only known that the life expectancy of needles increases as one moves from south to north (Serebryakov, 1961), but whether this phenomenon is related to the needle density of shoots is unknown. There are only single published patterns of changes in the proportion of needles in the leafy shoots of Scots pine in relation to the stem diameter at breast height, and they are directly opposite. In the conditions of the Ukrainian steppe, this relationship is negative (Sytnyk et al., 2017), and in the northern taiga subzone in the Arkhangelsk region it is positive (Babich et al., 2004).

The purpose of our research was to identify climate patterns of changes in the percentage of needles (*PL*, %) in the leafy shoots of Scots pine trees on the territory of Northern Eurasia. To achieve this goal, the following tasks were set:

- to compile the original database of *PL* in the leafy shoots of Scots pine;
- to develop a regression model of *PL* changes in relation to the dendrometric indicators of a tree and the climate variables of Northern Eurasia;
- to establish whether there is a difference between natural stands and plantations in the value of *PL*.

2. Material and methods

The harvest data on the *PL* of Scots pine from different regions in the amount of 558 sample trees, represented by both natural stands and plantations, were taken from the mentioned database (Usoltsev, 2020). The characteristics of the source material are given in Table 1. The mentioned database contains the coordinates of the sample plots where data on model trees were obtained. Using these coordinates, we determined the corresponding territorial indicators of the average January temperature and average annual precipitation from the corresponding climate maps (World Weather Maps, 2007). These climate maps were shown in our previous article (Usoltsev et al., 2022). The use of the maps of winter temperature instead of the average annual one was justified earlier (Usoltsev et al., 2019).

Table 1. Statistics of the analyzed indicators of 558 sample trees

Designation of statistics ^(a)	Indices analyzed ^(b)							
	<i>A</i>	<i>D</i>	<i>H</i>	<i>PL</i>	<i>LAT</i>	<i>LON</i>	<i>T</i>	<i>PR</i>
Ukrainian Polesie, natural stands								
Mean	141	45.8	31.1	51.6	49.7	30.3	-7	570
Min	64	27.0	23.0	37.3	-	-	-	-
Max	186	55.0	36.6	73.6	-	-	-	-
SD	39.8	7.4	3.9	9.7	-	-	-	-
CV, %	28.2	16.1	12.7	18.7	-	-	-	-
n	12	12	12	12	-	-	-	-
Ukrainian Polesie, plantations								
Mean	51	23.9	23.9	61.5	50.6	28.5	-8	570
Min	15	8.0	7.3	42.0	-	-	-	-
Max	91	38.1	33.7	76.3	-	-	-	-
SD	21.2	8.8	7.4	7.7	-	-	-	-
CV, %	41.2	36.8	31.1	12.6	-	-	-	-
n	24	24	24	24	-	-	-	-
Ukrainian steppe, plantations								
Mean	58	20.6	18.7	59.7	48.6	35.4	0	440
Min	9	7.0	4.5	49.8	-	-	-	-
Max	90	27.2	24.3	71.6	-	-	-	-
SD	26.3	6.0	6.5	6.8	-	-	-	-
CV, %	45.2	29.0	34.9	11.4	-	-	-	-
n	14	14	14	14	-	-	-	-
Central Urals, southern taiga, plantations								
Mean	24	10.1	10.1	66.5	57.0	62.0	-18	440
Min	15	2.4	3.0	41.3	-	-	-	-
Max	32	20.0	18.5	95.6	-	-	-	-
SD	6.2	4.7	4.2	11.3	-	-	-	-
CV, %	25.5	46.1	41.4	17.0	-	-	-	-
n	81	81	81	81	-	-	-	-
Southern Urals, southern taiga, natural stands								
Mean	79	21.8	19.7	73.4	55.5	60.2	-18	570
Min	44	7.0	8.3	33.6	-	-	-	-
Max	126	33.7	26.7	88.7	-	-	-	-
SD	17.7	7.4	5.5	8.0	-	-	-	-
CV, %	22.4	33.8	27.9	10.9	-	-	-	-
n	97	97	97	97	-	-	-	-
Western Siberia, forest steppe, plantations								
Mean	28	12.7	11.3	75.1	55.6	73.5	-20	320
Min	10	4.5	3.5	52.0	-	-	-	-
Max	50	21.0	19.6	83.0	-	-	-	-
SD	12.5	3.7	4.7	4.8	-	-	-	-
CV, %	44.0	29.4	41.6	6.4	-	-	-	-
n	147	147	147	147	-	-	-	-
Turgai depression, steppe, natural stands								
Mean	49	14.2	14.2	76.6	52.3	64.0	-14	300
Min	20	0.6	1.9	56.6	-	-	-	-
Max	110	34.5	26.1	88.0	-	-	-	-
SD	26.6	7.4	5.2	6.7	-	-	-	-
CV, %	53.8	51.7	36.5	8.8	-	-	-	-
n	84	84	84	84	-	-	-	-
Turgai depression, steppe, plantations								
Mean	41	13.2	12.5	73.5	52.3	64.0	-14	300
Min	22	2.6	3.5	45.6	-	-	-	-
Max	50	21.7	16.2	93.9	-	-	-	-
SD	13.0	5.4	4.1	9.6	-	-	-	-
CV, %	31.4	41.1	32.7	13.1	-	-	-	-
n	99	99	99	99	-	-	-	-

(a) Mean is mean value; Min is minimum value; Max is maximum value; SD is standard deviation; CV is coefficient of variation; n is number of observations.

(b) *A* is tree age, years; *H* is tree height, m; *D* is stem diameter at breast height, cm; *PL* is needle percentage in leafy shoot biomass, %; (*LAT*) and (*LON*) are geographical latitude and longitude, respectively, °; *T* is averaged January temperature, °C; *PR* is average annual precipitation, mm.

As mentioned above, the *PL* value is related to the stem diameter. In the conditions of the Ukrainian steppe, the pair relations of *PL* in 15 trees of the Scots pine and 15 trees of the introduced black locust (*Robinia pseudoacacia* L.) were analyzed not only with the stem diameter, but also with the tree age and height. Although all the dependences turned out to be statistically weak (Sytnyk et al., 2017), we need to find out what proportion of *PL* variability can occur on the dendrometric (mensurational) indicators of trees (age, diameter and height), on climatic variables (the average January temperature and average annual precipitation) and the origin of stands (natural and artificial).

When modeling the response of the biomass of two-needled pine trees to the January temperature and annual precipitation, taking into account the origin of stands, the affiliation of trees to natural stands and plantations was encoded by the binary variable, $B = 0$ and $B = 1$, respectively (Usoltsev et al., 2020). When we introduced only single binary variable B into the equation, this means that the 3-D surface (temperature – precipitation - biomass) in X-Y-Z coordinates shifts between natural and artificial trees only along the Z axis by the value of the regression coefficient at the binary variable B . According to our assumption, the biomass of trees in natural stands and plantations reacts differently to changes in the age because their differences in temporal stem growth (Zolotukhin, 1966; Jordan and Farnworth, 1982; Makarenko and Biryukova, 1982; Polyakov et al., 1986; Usoltsev & Vanclay, 1995; Romanov et al., 2014). In order to take these differences into account, in the designed model, along with B , we introduced the synergisms ($B \times \ln A$) as another independent variable. Although this synergism was not statistically significant, in our current case we consider it possible to include in the designed model for *PL*. To account for the simultaneous effects of temperature and precipitation, their product (synergism) was introduced in the equation for tree biomass as another independent variable, and it was statistically significant (Usoltsev et al., 2020).

3. Results and discussion

Based on the above and the harvest data, the statistical characteristics of which are shown in Table 1, we tested the following model structure:

$$\ln(PL) = a_0 + a_1(\ln A) + a_2(\ln D) + a_3(\ln H) + a_4[\ln(T+50)] + a_5(\ln PR) + a_6[\ln(T+50)] \times (\ln PR) + a_7(B) + a_8(B \times \ln A), \quad (1)$$

in which the regression coefficients a_1 , a_3 and a_6 for variables $(\ln A)$, $(\ln H)$ and $[\ln(T+50)] \times (\ln PR)$ according to the Student's criterion were not statistically significant at the level of $p < 0.05$ ($t = 0.6$, 1.1 and $1.1 < t_{05} = 1.96$) and were excluded from further analysis.

The final model has the form:

$$\ln(PL) = 7.1670 - 0.0273(\ln D) - 0.5074[\ln(T+50)] - 0.1631(\ln PR) - 0.4000(B) + 0.0899(B \times \ln A); \quad (2)$$

$\text{adj}R^2 = 0.335$; $SE = 0.10$,

where B is the binary variable encoding whether the harvest data belongs to natural stands ($B = 0$) or plantations ($B = 1$); $\text{adj}R^2$ is a coefficient of determination adjusted for the number of parameters; SE – equation standard error.

According to the Student's criterion, all regression coefficients in the model (2) are significant at the level of $p < 0.01$ ($t = 3.0 \dots 11.3 > t_{01} = 2.58$). Since the mean January temperature in the northern part of Eurasia has negative values, the corresponding independent variable is modified and subjected to log-log procedure as $(T+50)$. The intercept in model (2) is adjusted taking into account the logarithmic transformation (Baskerville, 1972). The contributions of mensuration variables (age and stem diameter), climatic variables (temperature and precipitation) and the origin of stands (natural and artificial) to explain the variability of the desired *PL* indicator by model (2) are 15, 53 and 30 %, respectively.

According to the sign of the independent variable ($\ln D$), the needle density of leafy shoots has a negative relationship with the stem diameter. Apparently, this pattern is associated with the concentration of needle biomass per unit of shoot length in trees that have lagged in growth (candidates for dying off) and have a relatively smaller stem diameter (Yablokov, 1934). The above is consistent with the result obtained in a 35-year-old Norway spruce stand: with the increase in stem diameter from 4 to 30 cm, the percentage of needles in the leafy shoot biomass decreases from 60 % to 50 % (Burger, 1939).

Judging by the sign of the independent variable (B), the needle density of leafy shoots in plantations is lower than in natural forests, and judging by the sign of the variable ($B \times \ln A$), the marked difference decreases or changes the sign as the age of the trees increases. This pattern is somewhat repeated when modeling the biomass of needles in plantations and natural stands, but with the opposite sign: at the young age, the biomass of needles in plantations is higher than in natural stands, but then with age there is a change in the ratio of biomass value, and natural stands gain an advantage over plantations in terms of the stock of needle biomass (Usoltsev & Vanclay, 1995).

Judging by the signs of the independent variables [$\ln(T+50)$] and ($\ln PR$), the PL indicator with unchanged values of age and stem diameter is negatively associated with both averaged January temperature and annual precipitation. The first pattern is explained by the increase in January temperature associated with a decrease in the moisture supply of territories in the direction from the taiga zone to the steppe, and the second one - by the increase in the climate continentality and the related decrease in moisture supply of forest areas in the direction from west to east (Nazimova, 1995). For the purpose of graphical interpretation of the named regularity, the average values of the age of a tree (46 years) and the stem diameter at breast height (15.6 cm) for all regions are substituted into the model (2). Then, according to the set values of January temperature and annual precipitation, the corresponding 3D surface for PL of natural stands and plantations is constructed (Fig. 4).

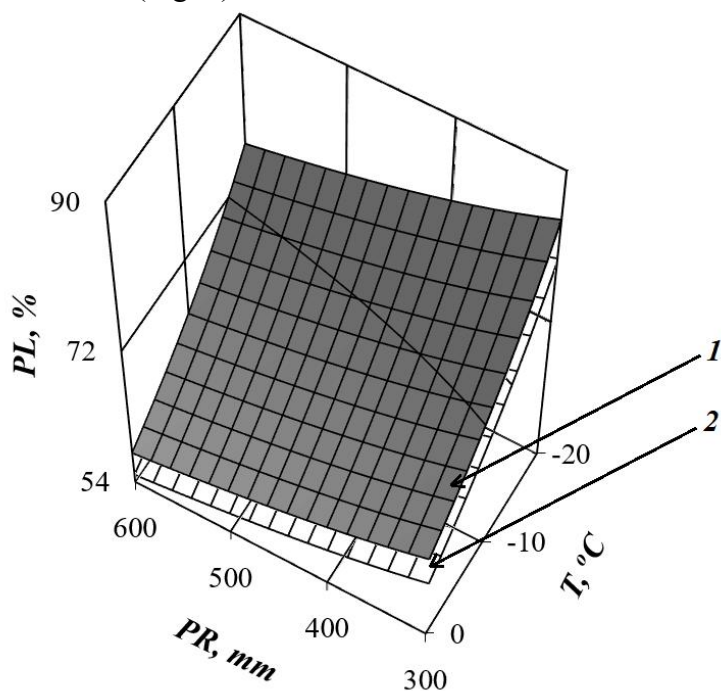


Fig. 4. The change in the theoretical values of PL in the coordinates of the average January temperature and average annual precipitation with the age of 46 years and the stem diameter of 15.6 cm; 1 - natural stands, 2 - plantations.

We can see in Fig. 4 that with unchanged values of age and stem diameter, PL in natural stands is higher than in plantations, and this difference is statistically significant. In both origins, PL increases with both a decrease in temperature and a decrease in precipitation. The analysis of Fig. 4

allows us to conclude that with a decrease in annual precipitation from 600 to 300 mm, there is an increase in PL by 0.2...0.3% for every 10 mm of annual precipitation, both in natural stands and in crops. When the January temperature decreases from 0 to -20 °C, PL increases by 0.8...1.0% for each 1°C.

In order to trace how the ratio of PL in plantations and natural pine forests changes with age, the auxiliary equation is calculated

$$\ln(D) = -1.6929 + 0.8144(\ln A) + 0.3396[\ln(T+50)] + 0.0114(\ln PR) + 0.8537(B) - 0.1846(B \times \ln A); \text{adj}R^2 = 0.552; \text{SE} = 0.34. \quad (3)$$

A graphical interpretation of equation (3) with average values of $T = -18$ °C and $PR = 570$ mm (Fig. 5) showed that at the initial stages of growth, the stem diameter in plantations is higher than in natural stands, but as the age increases, this ratio is reversed.

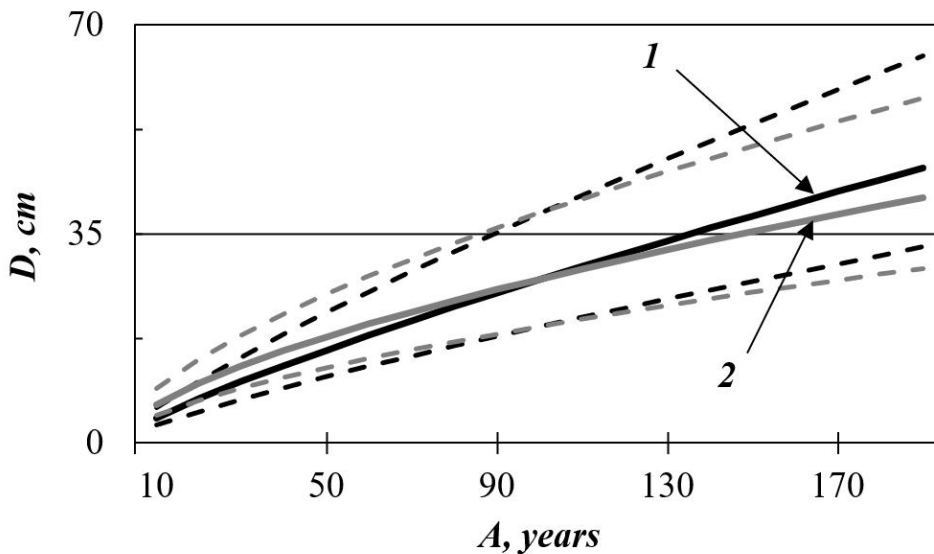


Fig. 5. The ratio of theoretical values of stem diameter at breast height in natural stands (1) and plantations (2) due to the age of the tree. The standard error of the equation is shown here and below

Substituting equation (3) into (2) and tabulating the resulting expression for the specified tree age at average values of $T = -18$ °C and $PR = 570$ mm, we obtained the age ratio of PL trees in natural stands and plantations (Fig. 6).

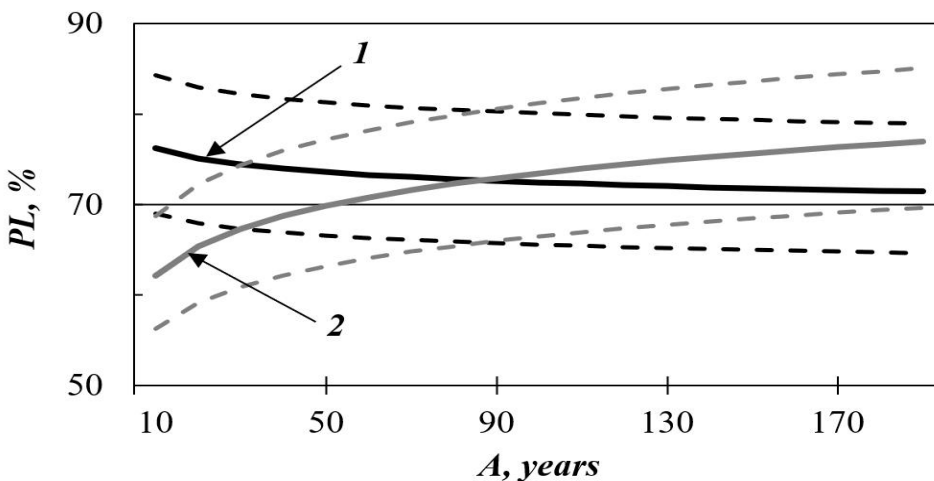


Fig. 6. Changes in theoretical PL values with the age of trees in natural stands (1) and plantations (2) at values $T = -18$ °C and $PR = 570$ mm.

Thus, it was found that at the initial stages of growth, *PL* in plantations is significantly lower than in natural stands, but as the age of trees increases, this ratio changes to the opposite. As noted above, in terms of the needle biomass, plantations and natural stands correlate in the opposite way: at the initial stages of growth, the biomass of needles is higher in plantations due to a higher growth rate, but with age, the growth rates are aligned or reversed and the ratio of the biomass of needles changes accordingly. This means that the increase in *PL* is associated with a decrease in the growth rate of trees: (1) both with an increase in age and with the degree of tree depression in the canopy, and (2) both with a decrease in temperature in the direction from south to north and with a decrease in precipitation in the direction from west to east.

4. Conclusions

Based on the analysis of published data, it was stated that as we approach the source of air pollution, the proportion of needles in the biomass of leafy shoots increases. It is also known that in the worst site classes, the biomass of needles, when other parameters being equal, is higher than in the best sites, and this is explained by a compensatory effect: a decrease in assimilation activity is compensated by an increase in the biomass of the assimilation apparatus.

On this basis, it is hypothesized that an increase in the proportion of needles in the biomass of leafy shoots can be considered as a reaction to the deterioration of growing conditions, regardless of the causes of this deterioration.

It was found that the increase in *PL* is associated with both an increase in age and the degree of suppression of the tree in the canopy. It can also be associated with a decrease in temperature in the direction from south to north, and with a decrease in precipitation in the direction from west to east. All these trends may be associated with a decrease in the growth rate of trees due to the deterioration of habitat quality.

Thus, an increase in the proportion of needles in leafy shoots can serve as a diagnostic sign of the degree of deterioration of growth conditions, regardless of whether this deterioration is associated with the degree of air pollution or with changes in climatic conditions.

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