BRANCHES AND THE ASSIMILATORY APPARATUS OF FULL-GROWN TREES OF DOUGLAS FIR (*Pseudotsuga menziesii* /M i r b./ F r a n c o) OF A DIFFERENT COENOTIC POSITION

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Abstract

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The paper deals with problems of crowns and of the assimilatory apparatus of Douglas fir. Crowns of two trees aged about 70 years of different coenotic (dominant–subdominant) and production (volume: minimum–maximum) position in a stand were analysed. The trees came from the experimental stand 41D7, Training Forest Enterprise "Masaryk Forest" Křtiny (altitude 430 m). Differences between Sample tree 1 (subdominant tree – V = 0.44 m3) and Sample tree 2 (dominant tree –V = 2.37 m^3) were found in the course of the analysis of height and diameter increment. Sample tree 1 was characterized not only by a shorter crown, both absolutely and relatively (in % of the stem length) but also shorter whorl branches and their lower number. While the crown of Sample tree 1 was created by 28 whorls with 3.5 branches/whorl, Sample tree 2 was created by 37 whorls and 4.5 branches/whorl. A different course was also found in case of needle distribution ($g \times m^{-1}$). A unimodal curve was typical of the dominant tree while the subdominant tree was characterized by an irregular multi-peak curve. Throughout the crown profile, Sample tree 1 showed higher values of foliage index (the proportion of needle DM to skeleton DM) than Sample tree 2. The total biomass of needles in Sample tree 1 and Sample tree 2 was 10.55 and 68.2 kg, respectively. Leaf area index (LAI) in Sample tree 1 amounted to 4.90 $m^2 \times m^{-2}$ and that in Sample tree 2 5.26 $m^2 \times m^{-2}$.

Key words: Douglas fir, biomass, crown, foliage, LAI

Introduction and analysis of problems

In the past, the study of biomass of forest trees was related particularly to the wood-producing function of forests (e.g. Vyskot, 1980). At present, the biomass of forest species is the subject of a number of studies assessing not only the wood-producing function through an economic framework but moreover, they assess biomass from the viewpoint of non-wood-producing functions. Thus, the study of biomass contributes substantially to understanding ecological relationships of the growth of forest trees which can result in a number of management measures (e.g. Chroust, 1993).

A number of data concerning the problems of Douglas fir crown biomass can be also found in available literature (e.g. Massman, 1981). These data are, however, sharply determined by used methods and, therefore, they are of limited (relative) information value.

For example, just Massman (1981) studying the distribution of foliage in Douglas fir crowns growing in the region of North America found that the maximum foliage density ($m^2 \times m^3$) occurred at about 80% of the height of the trees.

Gruber and Sowitzki (1995) analysed foliage of Douglas fir growing in the region of Germany. For example, the authors found that the weight proportion of proventive shoots in crowns amounted to 65%; in terms of the number of the shoots it was 75%. The mean duration of the "rest" of the proventive shoots ranged between 3 and 4 years.

Differences in the distribution of the assimilatory apparatus biomass in crowns of Douglas fir and white fir (*Abies concolor*) were studied by Schmid and Morton (1981). Their studies showed that while the biomass distribution in Douglas fir amounted to 1:3.5:2 that in *A. concolor* was 1:2:1.

The foliage distribution in crowns of Douglas fir growing in the region of the Netherlands was studied by Bartelink (1996). He found that the maximum vertical distribution of the foliage surface density ($m^2 \times m^3$) as well as of skeleton ($kg \times m^3$) in Douglas fir trees analysed by the author occurred at an age of 9–39 years approximately below the crown half.

Research presented in this paper can be ranked among similarly outlined studies. The main objective of our studies was to describe differences in the architecture of branches or in the amount and distribution of the assimilatory apparatus in their crowns on the basis of the destruction analysis of two mature sample trees of different coenotic position and volume.

Material and methods

Experimental stand

Stand 41D7 where extensive studies of particularly production and soil science character were carried out but also investigations aimed at the position of Douglas fir in the stand became a basis of the study.

The experimental stand is situated in the Training Forest Enterprise "Masaryk Forest" Křtiny at an altitude of 430 m. A typical mesotrophic Cambisol developed on granodiorite is a soil type there. It is a plateau of a gentle SE slope, forest type 3B2 – rich oak beech forest with woodruff. A various spatial and species composition (larch 26%, beech 20%, Douglas fir 18%, spruce 15%, pine 10%, oak 10%, birch 1%) became a main condition for the establishment of research thinning plots in the stand in the 60s. At present, the stand is about 75 years old and its total area amounts to 6.36 ha.

Methods

Methodical procedures of our studies were based on a paper "Determination of the distribution of needles in crowns of full-grown trees" (Čermák et al., 1990). For the purpose of our study, two Douglas fir sample trees were selected in the experimental stand, viz. Sample tree 1 (V1) represented a production minimum and at the same time subdominant trees and Sample tree 2 (V2) a production maximum and dominant trees. Both sample trees came from biogroups of similar species composition (V1– Douglas fir, beech, larch, spruce; V2 – Douglas fir, beech, larch, lime). The sample trees were analysed after their cutting down. Sample tree 1 was felled in autumn 2000 and Sample tree 2 was felled in early spring 2001. Actual partial methods can be divided into several in principle separate points:

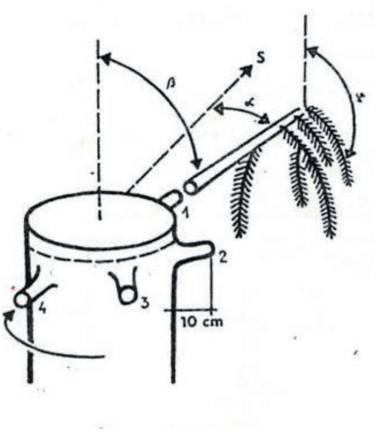


Fig.1. Procedure in the destructive analysis of crowns.

- Primarily after felling the trees, distances were measured between height whorls. On the basis of these data, it was possible to analyse the height growth of sample trees. From disks made at an age of 1.3 m from the tree foot, widths of annual rings were measured in four perpendicular directions. These data were used to analyse the diameter increment of sample trees. To determine the morphological form of a stem the stem diameter was measured at various distances (always by two metres from the tree foot or from breast height).
- All whorl branches in sample tree crowns were measured in detail. The procedure of measurement is given in Fig. 1. All branches between whorls were also measured and recorded.
- The amount and distribution of the assimilatory apparatus were studied according to sample tree branches. These were sampled as representative branches (mostly from the every third whorl) and analysed to particular year shoots in laboratory conditions. The amount, length and dry matter weight (at 80°C) of all shoots were recorded as well as needle DM according to needle year-classes and the respective shoot of a certain age of the given sample tree branch. For Sample tree 1, branches from the 4, 7, 10, 13, 16, 19, 22 and 26 whorls and for Sample tree 2, branches from the 1, 3, 6, 9, 12, 15, 18, 23, 28, 31 and 37 whorls were selected.
- The last stage of the study was the analysis of needles of selected age (always the first and/or next odd) from shoots of sample tree branches. Dry matter, specific surface and needle length were determined (always 20 needles in a sample). Data obtained could be intercompared. They also served for the determination of the total leaf projection area of sample trees and LAI values. The determined projection area (a parameter inevitable for the determination of LAI) for Sample tree 1 and Sample tree 2 amounted to 14.24 and 68.69 m^2, respectively.

Results and discussion

Basic parameters of both sample trees are given in Table 1. It is possible to say that the determined volume of the Sample tree 1 stem, i.e. a subdominant tree amounted to about 19% of the value of the Sample tree 2 volume.

T a b l e 1. Basic parameters of sample trees determined after their felling.

Parameters	Sample tree 1 (V1)	Sample tree 2 (V2)
Total length of stem (m)	27.1	35.1
Height of the end of crown (m)	20.0	19.8
Breast height diameter (cm)	21.3	48.0
Volume of stem (m^3)	0.44	2.37

Height growth of both sample trees is given in Fig. 2. Primarily, it is necessary to emphasize that the determined age of both sample trees was the same. The course of the sample tree height increment is very similar, however, particularly differences in absolute values are evident (the mean height increment of Sample tree 1 was only 41 cm in the studied period while the mean height increment of Sample tree 2 reached a value of 54 cm). Differences in the height increment of sample trees began to be differentiated about from the 25th year of age of the sample trees. Differences were also found in the current increment culmination. In Sample tree 1, it occurred in 11 years of age (93 cm) while in Sample tree 2 in 23 years of age (111 cm).

It is possible to note that Sample tree 1 began to differ in height from Sample tree 2 about from 25 years of age. Till then, vales of height increments were virtually the same. The reason of the fact can consist in genetic diversity or in the effect of environment (oppression by neighbouring trees). Decrease in the increment of Sample tree 1 resulted in the earlier culmination of height increment. It is possible to state that the course of height increment or growth of both sample trees corresponds to the growth patterns of trees (Assmann, 1968). Culmination of the current increment of Douglas fir trees growing on sites in the Czech Republic between 15 (10) and 30 years is also documented by research results published by Šika and Vinš (1978). Maximum values of the current increment determined by the authors exceeded 80 cm.

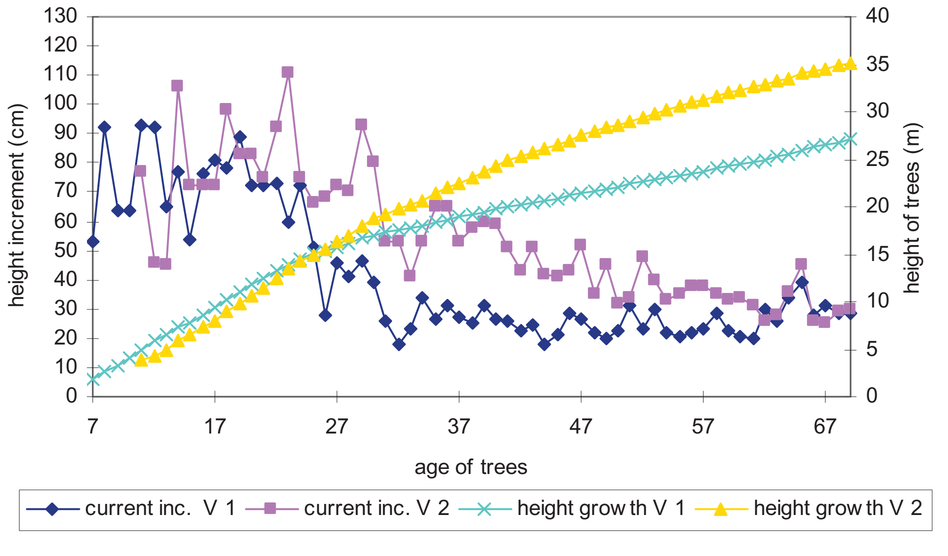


Fig. 2. Analysis of the height growth of sample trees.

Similarly as height increment also **diameter increment** of sample trees developed being determined by means of tree-ring analyses (see Fig. 3). The mean diameter increment (mean double width of annual rings) of Sample tree 1 on a basal area amounted to 3.0 mm, that in Sample tree 2 was 6.4 mm. It is of interest that in Sample tree 1, maximum diameter increment was higher (10.9 mm) than maximum diameter increment in Sample tree 2 (10.5 mm).

Thus, the course of the diameter increment supports deductions (see height growth) on the reduction of increment in Sample tree 1 as against the Sample tree 2 occurring at an age of about 25 years. It manifested itself in the different social position of both trees.

The diameter increment of Douglas fir trees in this stand was also analysed by Kantor et al. (2001). The study has shown that the culmination of current diameter increment in Douglas fir occurs very early, viz. at an age of about 10 years. Also in other Douglas fir trees in the stand, an increase in diameter increment was found at an age of about 25 years and further in last years. Similarly as in our study, a marked decrease of increment with only negligible growth between 45 and 65 years was found in subdominant trees. While in Sample tree 1, the mean width of annual rings reached 6.4 mm, in Sample tree 2 the value amounted to 119.0 mm.

On the basis of the comparison of height and diameter increments it is possible to conclude that in case of height increments, the highest differences occurred between 25 and 45 years of age whereas in case of diameter increments, the differences occurred between 40 and 60 years of age. Higher differences are also evident between the diameter growth curves and height growth curves. Thus, it is evident that the height increment of a sample tree is less dependent on the tree position than the diameter increment.

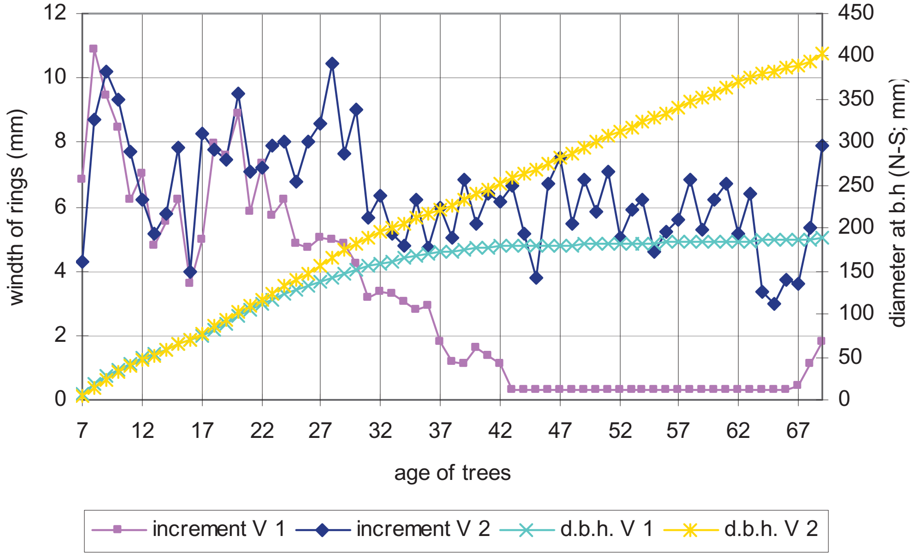


Fig. 3. Analysis of the diameter increment of sample trees.

Values of **form factors** of sample tree stems were as follows:
Sample tree 1 – true form factor 0.51; artificial form factor 0.46
Sample tree 2 – true form factor 0.48; artificial form factor 0.37.

Based on the figures it is evident that the stem of Sample tree 1, i.e. a tree growing predominantly as an subdominant tree was more non-tapering as against the stem of Sample tree 2 (a tree with a fully illuminated crown).

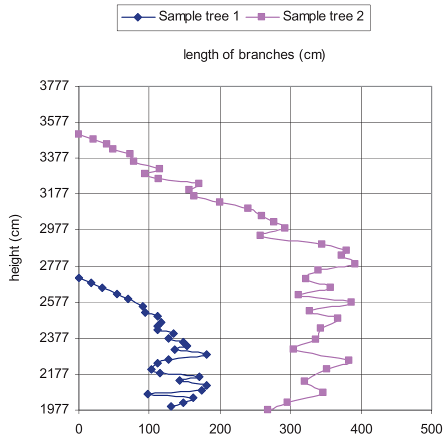
Branches in sample tree crowns

A detailed overview of crowns or **whorl branches** in sample tree crowns is given in Table 2. The table shows that the mean number of branches in the whorl of Sample tree 1 (3.5) was 1 branch lower than in Sample tree 2 (4.5). The mean length of branches in the whorl of Sample tree 1 was about 1.5 m shorter as compared with that in Sample tree 2. The percentage of a crown from the stem length in case of Sample tree 1, i.e. a subdominant tree, was markedly lower than in the dominant tree (26 and 44%, respectively). To compare crown lengths and mean lengths of whorl branches of both sample trees their ratio was used. While the proportion of the mean branch length to the crown length in Sample tree 1 amounted to 0.16, in Sample tree 2 the value amounted to 0.17.

T a b l e 2. Characteristics of crowns and whorl branches in sample trees.

Parameters	Sample tree 1	Sample tree 2
Crown length [m]	7.1	15.3
Crown length (precentage of stem)	26.3	43.7
Amount of whorl in crown	28	37
Amount of branches in crown	99	164
Mean numer of branches in the whorl	3.5	4.5
Total length of branches in crown	110	435
Mean length of branches	111	265

The architecture of crowns of sample trees is depicted in Fig. 4. The right figure shows a comparison of the actual length of whorl branches according to their absolute crown height, the left figure shows a comparison of the sample tree branch length according to their position in the tree crown. It is evident that the crown height in both sample trees was in principle the same, viz about 20 m. The subdominant tree crown 7.1 m in length reached virtually a half of the Sample tree 2 crown length which was 15.3 m long. The longest whorl branches in V1 occurred about 60% and next behind 80% of the crown length, in V2 it occurred already before 50% of the crown length. In places (about 24 m above the ground) where the subdominant tree showed the longest branches (even 1.8 m), the dominant tree showed markedly longer whorl branches (about 3.4 m).



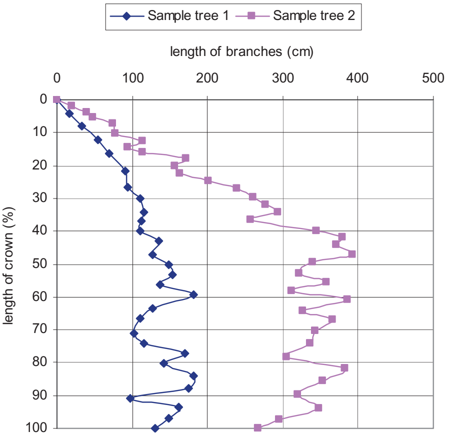


Fig 4a, b. The course of mean total lengths of whorl branches in crowns of sample trees: a) actual crown size, b) relative crown size.

Amount and distribution of the assimilatory apparatus

The total weight of needles of sample tree branches is given in Table 3. According to the table the highest weight of needles was found in branches of the central part of the crown. In case of the subdominant tree, it referred to a branch from the 16th whorl (in 59% of the crown length) – in case of the dominant tree, it referred to a branch from the 18th whorl (in 40% of the crown length). The determined highest value of Sample tree 1–199 g, is about 4.5× lower as against Sample tree 2 – 906 g. Based on the table, it is evident that lengths of these sample tree branches were not the longest from branches assessed. The longest branch in Sample tree 1 was a branch from the 26th whorl (232 cm, in 93% of the crown length) and in Sample tree 2 a branch from the 23rd whorl (431 cm, in 53 of the crown length).

In general, a maximum weight in the subdominant tree was lower, both in a relative crown (in 59 and 40%, respectively) and at the actual height above the ground (23 and 29 m, respectively).

Vertical distribution ($g \times m^{-1}$) was an indicator immediately related to the distribution of needles in crowns and thus to the weight of needles and length of branches. In both cases, the greatest value of distribution was found in branches with the greatest total DM of needles (the 16th whorl – V1 and the 18th whorl – V2). Thus, similarly as in weight, maximum values in the subdominant sample tree are lower than the dominant sample tree. The maximum value of distribution in Sample tree 1 (89 $g \times m^{-1}$) was 2.6× lower than in Sample tree 2 (231 $g \times m^{-1}$). In addition to absolute values the course of vertical distribution was also different. While in Sample tree 1, three-peak distribution “curve” was found with the highest first peak occurring about in 30% of the crown length, i.e. about 25 m above

T a b l e 3. The amount (g) and distribution ($g \times m^{-1}$) of needle biomass in sample tree branches.

Sample tree 1

Samples branches	Length of branches	Distance of whorls from the crown top	Total data			
			Weight of needles	Weight total	Distrib.	Distrib.
Number of whorl	cm	cm	g	g	($g \times m^{-1}$)	($g \times m^{-1}$)
4	69.5	116.0		55.96		80.52
7	134.0	214.5	135.38	135.79	101.03	101.34
10	166.5	284.7	100.31	104.85	60.25	62.97
13	154.0	358.5	125.10	128.70	81.23	83.57
16	216.0	422.3	191.98	198.72	88.88	92.00
19	107.0	506.4	65.09	67.09	60.83	62.70
22	170.0	571.3	73.98	74.79	43.52	43.99
26	232.0	666.0	180.58	186.15	77.84	80.24

Sample tree 2

Samples branches	Length of branches	Distance of whorls from the crown top	Total data			
			Weight of needles	Weight total	Distrib.	Distrib.
Number of whorl	cm	cm	g	g	($g \times m^{-1}$)	($g \times m^{-1}$)
1	20.0	30.0	1.36	1.36	6.80	6.80
3	59.0	84.0	6.39	7.93	10.83	13.44
6	109.0	191.0	82.16	88.98	75.37	81.63
9	175.5	276.0	187.72	194.17	106.97	110.64
12	195.5	378.0	315.98	323.10	161.63	165.27
15	272.0	489.0	579.19	595.79	212.94	219.04
18	382.5	610.0	882.41	906.21	230.70	236.92
23	431.0	808.0	659.39	684.82	152.99	158.89
28	321.5	1028.0	252.21	301.57	78.45	93.80
31	338.0	1198.0	130.30	211.14	38.55	62.47
37	267.5	1533.0	23.72	36.95	8.87	13.81

the ground and the lowest last peak (about in 90% of the crown length), in Sample tree 2, a unimodal "curve" was found with a maximum closely before 40% of the crown length, i.e. about at 29 m above the ground (see Fig. 5).

Based on these comparisons, it is possible to conclude differences in the architecture of branching between the subdominant tree and the dominant tree related to differences in light relationships. An abrupt decrease in distribution as well as in needle weight along the top in the dominant tree indicates that lower branches of the tree are to a great extent shaded just by dense foliage in the crown top. On the other hand, the subdominant tree responses particularly on light/shadow conditions by its asymmetrical crown and under the crown canopy of other species. In this connection it is possible to note that maximum values of distribution (g × m^{-1}) from studies carried out in the group of dominant and co-dominant trees by Barták et al. (1993) ranged between 40 and 50% of the crown relative height. Thus, similarly as in the case of our dominant tree. Also in their case, it referred to a unimodal distribution curve.

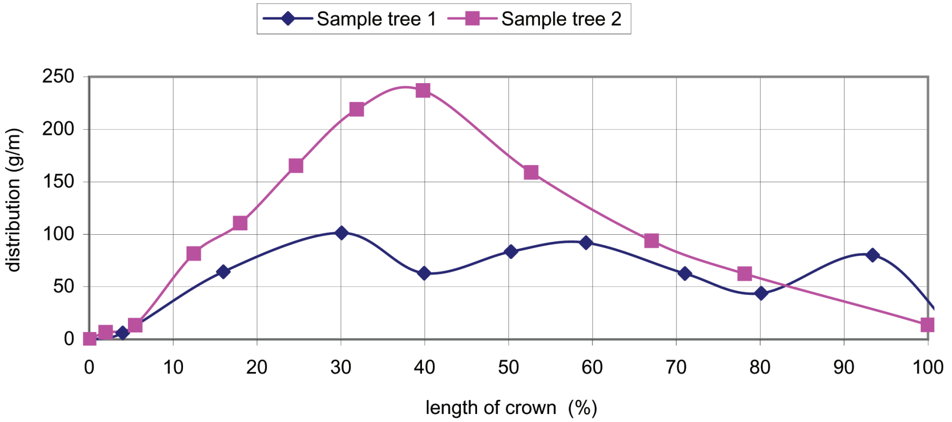


Fig. 5. Vertical distribution of the needle DM (g × m^{-1}) for both sample trees.

Another indicator under study was **foliage index** (g × g^{-1}). This index was calculated for every sample tree branch as the proportion of DM of needles and DM of skeleton. Also in this case, differences were found between both sample trees which was depicted in Fig. 6. Virtually throughout the crown, higher values of the index, i.e. the higher proportion of needles corresponding to the same weight proportion of a skeleton were found in Sample tree 1. Most likely, it is caused just by the subdominant position of the tree and thus lower photosynthetic performance of needles. The difference is more marked if we take into consideration the absolute crown height. For example, in case of the index value for the 7th whorl branch of Sample tree 1 (1.30) and for the 28th whorl branch of Sample tree 2 (0.11), that is roughly at the same height above the ground (about 25 m), the difference is almost 12-fold.

The maximum index value for Sample tree 1 (1.46) was found in the sample tree branch from the 4th whorl, i.e. at a height of about 26 m above the ground. In Sample tree 2, the maximum (0.94) was found in a branch from the 2nd whorl, that is between 34 and 35 m above the ground – again in the crown top. On the other hand, minimum values of the index were found at the crown base of both sample trees which is probably related to the fall of older needles at the base of crowns and in principle constant weight of the skeleton of the branches.

Also Fig. 6 (similarly as Figs 4 and 5) shows the different course of curves of both sample trees related to the different architecture of the dominant and subdominant tree.

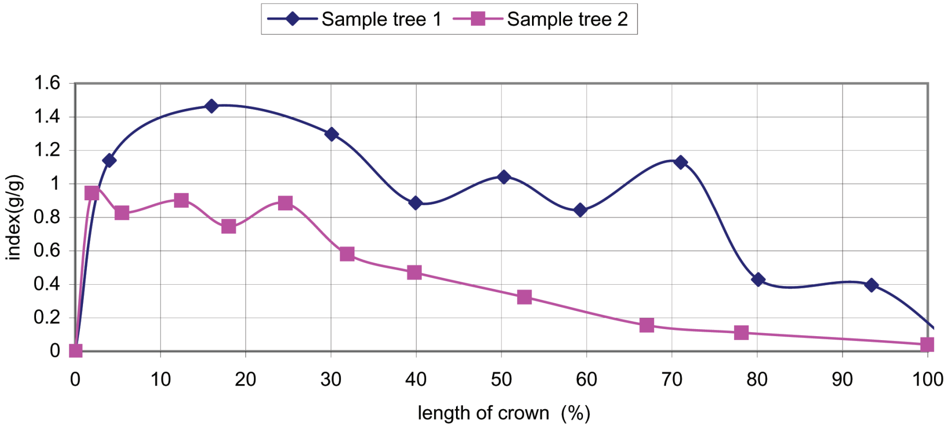


Fig. 6. Diagram of the course of the index of foliage of both sample trees.

The data obtained made possible to calculate **the total biomass of needles** of whorl branches as well as inter-whorl branches. The total DM of needles in Sample tree 1 reached 0.55 kg of which whorl branches amounted to 9.80 kg, i.e. about 93%. The total weight of needles of Sample tree 2 was 68.20 kg, whorl branches of the sample tree amounting to about 90% of weight (61.72 kg). It is possible to say that the total DM of needles similarly as the needle weight of whorl branches of Sample tree 1 amounted to about 16% of the needle DM of Sample tree 2.

It is also possible to compare relative amounts of the needle biomass in relation to the stem volume. An index calculated in this way ($m^3 \times kg^{-1}$), i.e. the proportion of the stem volume to the needle DM amounted to 0.042 in Sample tree 1 and 0.034 in Sample tree 2. Higher values of the index in Sample tree 1 indicate a need of the higher amount of needles per the stem volume unit. Thus, it is possible to speak about the relatively higher proportion of needles in the subdominant tree in relation to the stem volume.

Here, it is possible to mention results published by Vyskot (1981). The author mentions the following average DM of needles for three groups of sample trees of spruce aged about 60–70 years: 58.5 kg, 4.7 kg and 18.1 kg. Thus, a broad range of values. Schmid and Morton (1981) who analysed the biomass of foliage in 10–15 m tall Douglas fir trees growing in New Mexico came again to the broad spectrum of values, i.e. 14–38 kg DM of needles/tree.

Attention was also paid to the **proportion of particular needle year-classes** in the needle biomass. First, it is necessary to mention that 12-year-old needles in Sample tree 1 and 15-year-old needles in Sample tree 2 are the oldest needles. The amount and proportion of these needles were, however, negligible in total balance. The proportion of needles of particular needle year-classes in parts of crowns represented by sample tree branches is depicted in Figs 7 and 8.

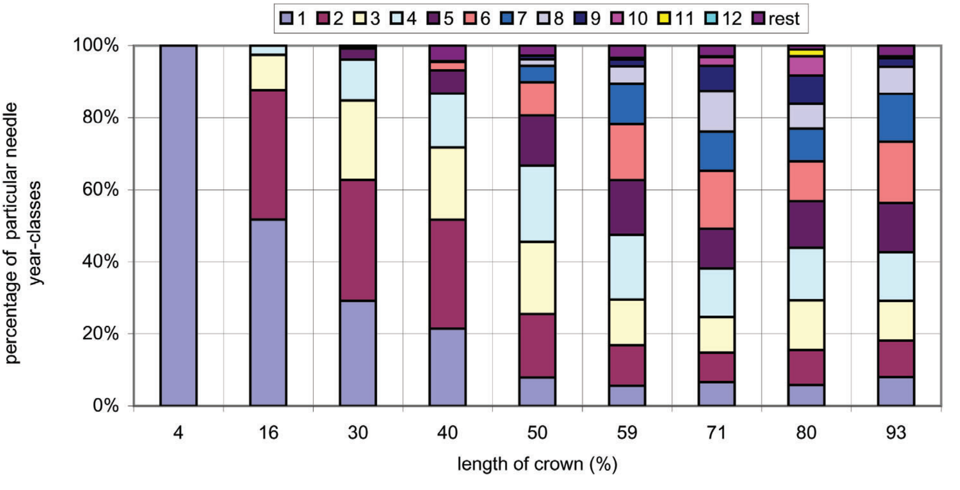


Fig. 7. The percentage of particular needle year-classes in various parts of the crown (% represents the relative distance of whorls from the crown top) of Sample tree 1.

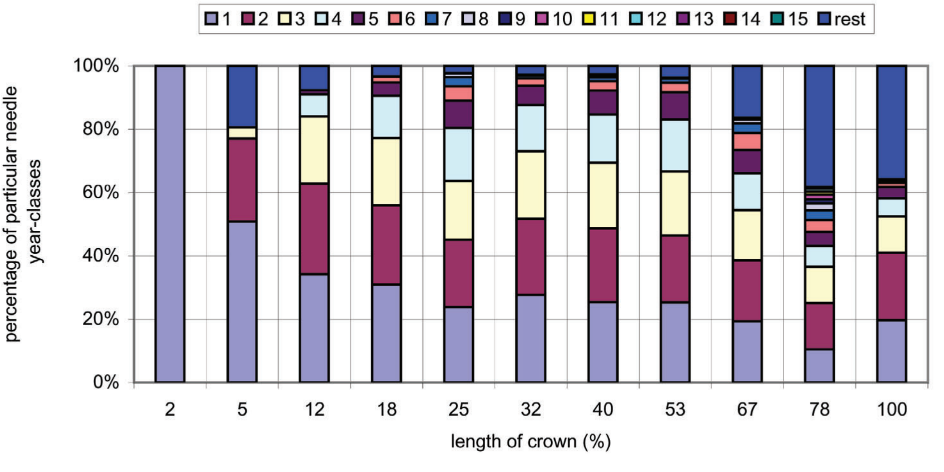


Fig. 8. The percentage of particular needle year-classes in various parts of the crown (% represents the relative distance of whorls from the crown top) of Sample tree 2.

Based on the conversion of the proportion of particular needle year-classes of sample tree branches for the whole sample tree, in Sample tree 1 the highest proportion corresponded to the second needle year-class (2.02 kg – about 20%). The first and the third needle year-class were represented roughly identically, viz. about 16% (1.56 kg). From the fourth needle-year, a decrease in the needle proportion with their age occurs (4^{th} needle-year – 14%, 5^{th} needle-year – 10%, 6^{th} needle-year – 9%, 7^{th} needle-year – 6% and ≥ 8^{th} needle-year – 6%). In Sample tree 2, however, there is an unambiguous decrease in the proportion of needles with their age. The first needle-year is represented most, viz. 24% (14.98 kg) being followed by the second needle-year with 22% (13.44 kg), the third needle-year amounts to 19% (12.00 kg), the fourth 15%, the fifth 7% etc. It is of interest to compare the proportion of the youngest four and older needle year-classes in the total balance of the needle weight of sample trees. From the fifth needle-year, a turn occurs when Sample tree 1 shows relatively higher proportion of needles as compared with Sample tree 2 and, on the other hand, there is the highest difference in the amount of older and younger needles. In Sample tree 1, needle-years aged 5 years and more create 31% DM of needles whereas in Sample tree 2, it is only 13%.

Thus, it is possible to conclude that the subdominant tree significantly differs from the dominant tree by the proportion of particular needle year-classes or by the higher proportion of older needle-years. It has been demonstrated that there are different strategies in the "uptake" of light caused by situation in the crown canopy when the subdominant tree or the biomass of its foliage respond to light conditions under the canopy while the dominant tree is more affected by its own crown.

Parameters of the assimilatory apparatus

The length and weight of sample tree needles were assessed by a common denominator, viz **specific weight** (mg × cm^{-1}). Based on results of the study (see Table 4) it is evident that an increase in values of the variable occurred in both sample trees with the age of needles and further from the crown base to the crown top.

Greater values of the specific weight of older needle year-classes can be probably related to the earlier needle fall of lower weight. On the other hand, the decrease of weight in needles of the same needle year-class but growing lower in the tree crown is related to ontogenesis (Chroust, 1993).

If we compare values of the specific weight of needles of particular sample trees it is possible to conclude that Sample tree 2, i.e. the dominant tree demonstrated values of the variable higher than that in Sample tree 1. It can be documented in case of the first needle year-class when in the subdominant tree, values of the specific weight ranged between 2.2 and 1.2 whereas in Sample tree 2, it was between 3.7 and 1.6. It was demonstrated that values of the specific weight of both sample trees did not differ markedly at the same height above the ground.

In the same sample trees where the specific weight of needles was studied also their **specific surface** was determined. Also there, an increase in the variable occurred with the

T a b l e 4. Specific weight of odd needle year-classes (mg × cm^{-1}) of whorl branches of sample trees.

Sample tree 1

Sample branches	Specific weight of needle (mg × cm^{-1})		
	1 year	3 year	5 year
top	2.22	2.50	
7	1.93	2.13	2.32
10	1.74	2.18	2.15
13	1.39	1.87	2.29
16	1.31	1.79	2.13
19	1.34	1.79	1.90
22	1.21	1.55	1.92
26	1.25	1.52	1.56
Mean	1.56	1.92	2.05

Sample tree 2

Sample branches	Specific weight of odd needle (mg × cm^{-1})				
	1 year	3 year	5 year	7 year	9 year
1	3.70				
3	2.04				
6	2.11	2.91			
9	2.28	2.91			
12	2.07	2.49	2.90	2.94	3.27
15	2.05	2.56	3.01	3.09	3.34
18	2.04				
23	1.92	2.34	2.76	2.91	
28	1.61	2.20	2.49		
31	1.59	1.78			
37	1.68				
Mean	2.01	2.42	2.78	2.98	3.31

needle age till the 5th needle year-class. In older needles, values of the specific weight ranged within the interval of younger needle-years (see Table 5 – Sample tree 2). As compared with the specific weight, however, at the specific surface a positive decrease in values did not occur from the crown top to its base. The course of values of the specific surface shows rather fluctuating and more or less balanced trend.

If we compare both sample trees it is possible to note higher balance in values as against the specific weight. For example, Sample tree 1 showed values of the specific surface of the first needle year-class in the range 0.18–0.23 cm^2 with the highest values for needles from the 10th and the 26th whorl branch. On the other hand, Sample tree 2 showed the highest values only two tenths higher (0.25 cm^2 – the 3rd whorl branch) and the minimum value was even four tenths lower (0.14 cm^2 – the 6th whorl branch) as compared with Sample tree 1.

T a b l e 5. Specific surface of selected needle year-classes (cm^2) of particular whorl branches.

Sample tree 1

Sample branches	Surface of needle (cm^2)		
	1 year	3 year	5 year
top	0.22	0.26	
7	0.22	0.27	0.27
10	0.23	0.28	0.28
13	0.22	0.25	0.27
16	0.19	0.29	0.31
19	0.22	0.28	0.29
22	0.18	0.21	0.22
26	0.23	0.27	0.25
Mean	0.21	0.26	0.27

Sample tree 2

Sample branches	Surface of needle (cm^2)				
	1 year	3 year	5 year	7 year	9 year
1	0.15				
3	0.25				
6	0.14	0.20			
9	0.18	0.19			
12	0.16	0.19	0.18	0.17	0.19
15	0.21	0.25	0.26	0.21	0.22
18	0.21				
23	0.20	0.25	0.27	0.23	
28	0.22	0.24	0.27		
31	0.23	0.27			
37	0.21				
Mean	0.20	0.23	0.24	0.21	0.20

Based on the data obtained the total projection leaf area of sample trees was determined. The value amounted to 69.8 m^2 for Sample tree 1 and 361.2 m^2 for Sample tree 2. Thus, the value of this variable for Sample tree 1 was in the same relation as the value of volume of this sample tree to Sample tree 2, i.e. 19%. An overview on the distribution of leaf area in crowns of sample trees is depicted by Figs 9 and 10. Also there, differences between sample trees representing different social position are evident. While in Sample tree 1, asymmetrical "multipeak" distribution was found, in Sample tree 2 in principle unimodal continuous distribution was found with a peak about in the crown half. A maximum in V 1 amounted to 4.4 $m^2 \times whorl^{-1}$ and in Sample tree 2, it reached 21.2 $m^2 \times whorl^{-1}$, i.e. about 4.8 × higher.

Differences in the LAI (leaf area index) value of both sample trees were not so considerable amounting to only 7%. Sample tree 1 exhibited LAI 4.90 $m^2 \times m^{-2}$ while Sample tree 2 5.26 $m^2 \times m^{-2}$.

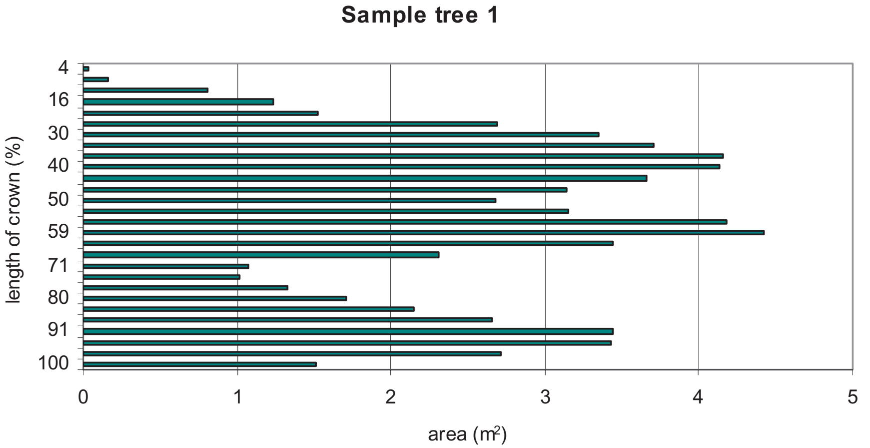


Fig. 9. Area of the needle surface in whorls (expressed in relative lengths of a crown) of Sample tree 1.

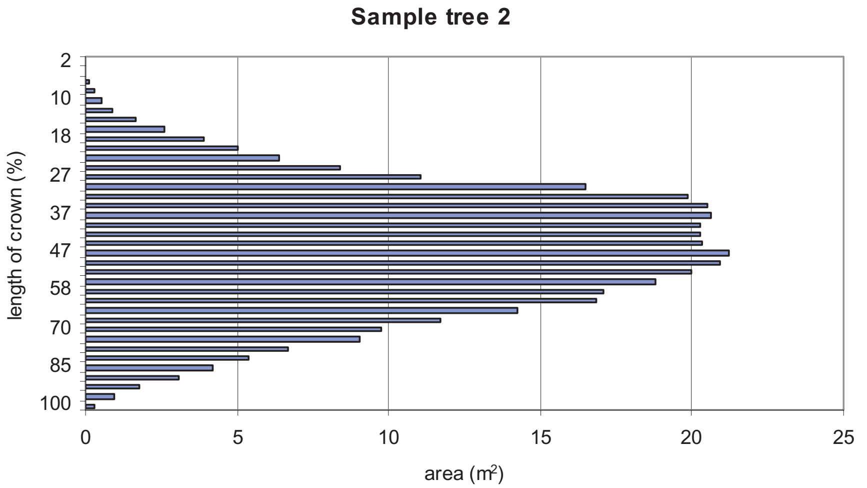


Fig. 10. Area of the needle surface in whorls (expressed in relative lengths of a crown) of Sample tree 2.

Conclusion

In conclusion, it is possible to remind once again differences between both sample trees representing subdominant trees and at the same time the production minimum (V1) and dominant trees with the production maximum (V2). Differences in the height and diameter increment of sample trees resulting in their different development and finally also position began to differentiate markedly at about the 25^{th} year of their age. During an analysis, the crown of the subdominant tree was shorter than that in the dominant tree at an age of 69 years, viz both relatively (in relation to the stem length) and absolutely. Also the total length of all whorl branches and the mean number of the branches/whorl were lower in the tree. Moreover, the subdominant tree differentiated from the dominant tree by the asymmetrical distribution of biomass as well as the area of the needle surface in the crown, by the natural smaller amount of needle biomass and by the higher foliage index of whorl branches. In the subdominant tree, the relatively higher proportion of older needles was found (over 5 years) than in the dominant tree. In Sample tree 1, lower values were also found in case of the specific weight of needles. On the other hand, the boundary of values of the specific surface did not substantially differ in both sample trees. Differences in LAI were only 7%.

Summary

The paper deals with problems of the biomass of needles including its distribution in crowns of Douglas fir in relation to the coenotic position. The study was carried out using the method of destruction analysis. For the analysis, two sample trees of Douglas fir were selected from the experimental stand 41D7 (age 69 years), Training Forest Enterprise Křtiny (SLT 3B), representing different coenotic position (subdominant and dominant trees) and volume stratification of the stand (volume minimum and maximum).

Primarily, the course was analysed of the diameter and height increment of both sample trees. In the studies, it was found that values of both the variables began to differ markedly roughly at an age of 25 years. It is possible to suppose that these differences resulted finally in the different position of trees in the stand.

Differences between the subdominant and the dominant tree were found in the length and architecture of crowns. For example, the relative length of the Sample tree 1 crown was 26%, in Sample tree 2 it was 44%. In Sample tree 1, 3.5 branches corresponded to one whorl, in case of Sample tree 2, on average one branch more corresponded to one whorl. Only the crown height was the same, namely about 20 metres.

The different position of trees in the stand was also manifested in the amount and distribution of the assimilatory apparatus in crowns of sample trees. In case of the dominant tree, a symmetrical distribution with a maximum 231 $g \times m^{-1}$ was found at about 30% of the crown length. In the subdominant tree, the maximum 89 $g \times m^{-1}$ was found at about 40% of the crown length.

Also in case of values of the foliage index ($g \times g^{-1}$) of whorl branches differences were found between the sample trees. Values of the index were substantially higher throughout

the crown in Sample tree 1 (0.40–1.46) than in Sample tree 2 (0.04–0.94). The total DM of needles of whorl branches of Sample tree 1 amounted to 9.8 kg, that in Sample tree 2 was 61.7 kg. Moreover, the relatively higher proportion was found of older needles in the total DM of needles in Sample tree 1. In the tree, these needles (aged over 5 years) amounted to 31% of the needle DM whereas in Sample tree 2, the needles amounted to only 13%.

Parameters of the assimilatory apparatus were last variables under study. Values of the specific weight of the last needle year-class ($mg \times cm^{-1}$) of Sample tree 1 ranged between 1.2 and 2.2, in Sample tree 2 between 1.6 and 3.7. Older needle year-classes showed higher values in both cases.

In case of the specific surface (cm^2), differences in values between the sample trees were not so marked as in the specific weight. Also an increase in the specific surface with the age of needles was not so positive.

The total projection area of Sample tree 1 was 69.8 m^2 and that of Sample tree 2 was 361.2 m^2. The LAI ($m^2 \times m^{-2}$) of Sample tree 1 and Sample tree 2 amounted to 4.90 and 5.26, respectively.

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