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Dynamics of tree species composition and characteristics of available space utilization in the natural forest of the National Nature Reserve Hrončokovský Grúň

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ABSTRACT: The paper deals with changes in the diameter structure of particular tree species as well as with the selected production characteristics in the mixed virgin forest Hrončokovský Grúň. The object of the analysis was the diameter structure of particular tree species in developmental stages of virgin forest. The data were collected in the years 1972, 1982, 1992 and 2002 on permanent research plots 71.5 × 70 m (0.5 ha) in size. Diameter frequencies for particular tree species were approximated with the curves. The goal was to evaluate their mortality or vitality according to the strength of the correlation in developmental stages of the virgin forest. A strong correlation was confirmed in the advanced phase of the growth stage, whereas the strongest correlation was recorded for the ash. Beech as a virgin forest bearer had a medium strong correlation. For the advanced phase of the optimum stage lower values of the correlation coefficients were determined for all tree species. The growth vitality and thus lower mortality was characteristic of maple and ash. Beech as a structure bearer is characterized by higher mortality and therefore a weaker correlation. In the breakdown stage the highest mortality was found for the fir, which is confirmed by the lowest value of the correlation coefficient. In the advanced phase of the optimum stage the highest mortality was recorded for the beech. The analysis of growth and production relationships was conducted on the transects of 3 permanent research plots 10 × 71.5 m in size (i.e. total size of 2,145 m^2). The analysis of the growth relationships between the crown and stem volume confirmed a strong correlation for beech and fir despite the fact they are present in the entire height profile of the virgin forest. The reason is that both of them are the shade-tolerant tree species. High correlation coefficients for maple and ash (R = 0.82 and R = 0.84) are the evidence of a distinctive influence of the assimilatory apparatus on the stem volume. The reason is the fact that both tree species are situated in the upper tree layer and have relatively enough space for the crown growth. The productive utilization of the crown space in the virgin forest confirmed the dominance of the beech as a structure bearer.

Keywords: natural forest; developmental stage; utilization of production space; structure

Variable tree species composition is a typical feature of primeval forests in the 4th and 5th vertical forest vegetation zone (Saniga 2004). Diverse forest ecosystems are characterized by complicated internal relationships resulting from different ecological requirements of individual tree species, their different growth capabilities and different physical age they can reach. This is reflected in stand structure as well as in the character and course of developmental processes. Volume and quality of produced biomass, and fulfilling the non-production functions depend on the stand structure (Saniga 2004), the formation of which is determined by regeneration processes in natural as well as in commercial forests. The higher the number of tree species in both the adult stand and young growth, the more demanding and complicated the regeneration phytotechnique. In natural forests, the course and extent of regene-ration processes are affected by physical mortality of individual tree species. Re-

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liable information on natural regeneration patterns allows the application of underlying mechanisms in shorter time spans within the framework of close to nature silviculture (Korpeľ 1989, 1995; Korpeľ, Saniga 1995).

As regards the tree species composition of the primeval forest in the National Nature Reserve (NNR) Hrončokovský Grúň, this primeval forest represents the culmination of tree species diversity (Korpeľ 1995). This tree species composition is a basic prerequisite for the markedly diversified spatial structure of a natural forest (Korpeľ 1995). The first results about the formation and volume of coarse woody debris within the developmental cycle were published by Saniga and Schütz (2002). The authors found that in the primeval forest of the NNR Hrončokovský Grúň, which belongs to the most species-diversified virgin forests of the 4th and 5th vegetation zones (six tree species), the necromass volume is high within the whole developmental cycle, reaching the highest values in the optimum stage. A significant increase of dead wood at this stage is caused by the phase shift of silver fir, dying back in the second developmental cycle compared to beech as a determinant tree species of this natural forest.

Regeneration processes of individual tree species in this primeval forest are further complicated partly because of different ecological requirements of individual tree species during germination, establishment and growth of seedlings (Korpeľ 1995; Saniga 2004).

The Hrončokovský Grúň primeval forest with its diverse tree species composition and differentiated physical ages of trees has some specific features. In addition to the fluctuation of the biomass volume, caused by the competition pressure of individual tree species and different maximum physical age, significant differences were found in the processes of the formation and structure of dead wood. A significant increase in the necromass volume in the optimum stage, confirming the observations of Saniga and Schütz (2002), is caused by high production potential and longevity of fir, which survives until the second developmental cycle, where beech is the main species. Fir is the predominant species of the standing necromass, which reflects its high static stability, whereby the gradual decline of living trees is caused by their high age (the breakdown stage). In the breakdown stage, there is a period with unsuitable ecological conditions for the establishment and growth of the subsequent generation resulting from different maximum physical ages of tree species and their different vitality. A continuous regeneration process starts at the time when a tree species dies out, which forms a gap in the available crown space of the size of a group at least (0.02 ha).

The papers dealing with research on virgin forests composed of more tree species were mainly focused on the diameter structure and on the growth processes of particular tree species (Jaworski, Skrzysewski 1995; Jaworski, Strzeska 2001; Jaworski et al. 2005). The utilization of productive growth space by the tree species and the relations between crown and stem volume were studied above all in selection forests (Saniga, Vencúrik 2007). The analysis of growth space economy by particular tree species on tending research plots, i.e. what the relationship between the tree and the stand productivity is like, was presented by Utschig (2002). The results confirmed a significant relationship between the increase in the tree growth space and the stem volume increment.

Growth and competition relationships between the tree species with different ecological demands on light and nutrients in the virgin forests have not been presented in the literature yet.

The objective of this study is to answer the following questions:

- How is the production space utilized by crowns of different tree species in individual developmental stages of natural forest and what is its dynamics within the time span of 30 years?
- What is the temporal change of canopy closure in individual developmental stages?
- How does the tree species composition change during 30 years, according to developmental stages?
- To assess the growth potential of individual tree species within the production space of a natural forest, an analysis of crown and trunk volumes was performed.

MATERIAL AND METHODS

The National Nature Reserve Hrončokovský Grúň was established in 1964. The area is 55.30 ha with a protection zone of 112.83 ha. The reserve is situated in the forest management unit Hronec, compartments 298, 299, 300 and 301. It is located in the geographical unit Slovenské Rudohorie Mountains in Central Slovakia (48°43'N, 19°35'E), the altitudes range between 730 and 1,050 m a.s.l., slope aspect is east to southeast, and slope angle ranges from 15° to 25°.

The average annual temperature is 5°C, precipitation totals are 800 to 850 mm per year. The bedrock is formed of andesite tuff agglomerates and pyro-

Table 1. The utilization of available growth space according to tree species and levels in the natural forest of NNR Hrončokovský Grúň in a time span of 30 years (growth stage) (PRP 1)

Year	Upper level		UAS_s/UAS_L	Intermediate level		UAS_s/UAS_L	Total		UAS
	species	C_{kd} (m^3)	(%)	species	C_{kd} (m^3)	(%)	species	C_{kd} (m^3)	(%)
1972	Spruce	1,655.76	17.76	Spruce	13.07	0.14	Spruce	1,668.83	8.95
	Beech	1,305.58	14.01	Beech	221.1	2.37	Beech	1,526.68	8.19
	Maple	1,215.79	13.04	Maple	22.09	0.24	Maple	1,237.88	6.64
	Fir	75.16	0.81	Fir		0.00	Fir	75.16	0.40
	Total	4,252.30	45.62	Total	256.26	2.75	Total	4,508.55	24.18
1982	Spruce	1,735.12	16.98	Spruce	68.68	0.67	Spruce	1,803.80	8.83
	Beech	1,900.25	18.60	Beech	179.71	1.76	Beech	2,079.96	10.18
	Maple	1,249.23	12.23	Maple	33.01	0.32	Maple	1,282.24	6.27
	Fir	123.37	1.21	Fir		0.00	Fir	123.37	0.60
	Total	5,007.97	49.01	Total	281.40	2.75	Total	5,289.37	25.88
1992	Spruce	1,755.27	16.77	Spruce		0.00	Spruce	1,755.27	8.39
	Beech	2,618.33	25.02	Beech	226.19	2.16	Beech	2,844.52	13.59
	Maple	872.51	8.34	Maple	37.63	0.36	Maple	910.14	4.35
	Fir	50.29	0.48	Fir		0.00	Fir	50.29	0.24
	Total	5,296.40	50.61	Total	263.82	2.52	Total	5,560.22	26.57
2002	Spruce	2,038.88	19.31	Spruce		0.00	Spruce	2,038.88	9.66
	Beech	3,105.07	29.41	Beech	386.85	3.66	Beech	3,491.92	16.54
	Maple	1,060.15	10.04	Maple	172.03	1.63	Maple	1,232.18	5.84
	Fir		0.00	Fir		0.00	Fir		0.00
	Total	6,204.10	58.76	Total	558.88	5.29	Total	6,762.98	32.03

C_{kd} – crown volume, UAS_s – utilization of the available crown space of tree species, UAS_L – utilization of the available crown space of level, UAS – total utilization of available crown space

clastics. The predominant soil types are Eutric and Dystric Cambisols, soil is sandy to loamy, with a low share of rocks, well aerated, well drained, fresh, moderately deep to deep, moderately acidic, with a low content of available nutrients.

Four phytosociological units (groups of forest types) are represented in the reserve: *Abieto-Fagetum, Fageto-Abietum, Fageto-Aceretum* and *Fraxineto-Aceretum*. Except for *Abieto-Fagetum* belonging to the 5th fir-beech forest vegetation zone and represented by the forest type *Filices – Asperula odorata – Oxalis acetosella – Prenanthes purpurea,* all remaining plant communities belong to the 6th spruce-beech-fir forest vegetation zone. In terms of the tree species composition, this natural forest is composed of European beech *(Fagus sylvatica* L.*)*, silver fir *(Abies alba* Mill.), Norway spruce (*Picea abies* L. Karst.), sycamore maple (*Acer pseudoplatanus* L.), European ash (*Fraxinus excelsior* L.) and wych elm (*Ulmus glabra* L.) and belongs to the most tree-species-diversified forest ecosystems in Europe.

The analysis of changes in the tree species composition in particular diameter classes according to the developmental stages of the virgin forest within a 30-year period was based on data from the full callipering of the permanent research plots, calculated per 1 ha. Developmental stages were identified according to the diameter structure at the establishment of permanent research plots by professor Korpeľ. In subsequent decades the measurements and evaluations of permanent research plots were repeated periodically.

The utilization of productive growth space of the virgin forest by particular tree species and the share of the tree species in the total crown canopy in tree layers were calculated according to data from the transects of PRP (715 m^2) in the particular decades of measurement (1972–2002). These dendrometric characteristics were measured:

- tree height (h) – to the nearest 0.5 m,
- crown base height (h_Z) – to the nearest 0.5 m,
- dbh – to the nearest 1 mm,
- crown width – four directions x_1–x_4, to the nearest 0.1 m,
- position of the tree – orthogonal coordinates x, y, to the nearest 0.1 m.

The analysis of the relation between the crown volume and the stem volume according to the tree species was based on data from the transects and years of measurement for the entire developmental cycle of the virgin forest.

Assmann's (1961) formula was used for the calculation of crown volume (C_k):

For broadleaved species:

$$C_k = \frac{\pi}{8} b^2 l \quad (m^3)$$

For coniferous species:

$$C_k = \frac{\pi}{12} b^2 l \quad (m^3)$$

where:
b – crown diameter (m),
l – crown length (m).

The crown (C_L) volume within the level was calculated as the sum of volumes of all crowns in the transect:

$$C_L = \sum C_k \quad (m^3)$$

The available crown space (V_L) of the particular level was calculated using the following formula:

$$V_L = S_{tr} \times \frac{h_0}{3} \quad (m^3)$$

where:
S_{tr} – area of transect (m^2),
h_0 – upper tree height (m).

The upper tree height is defined as the average height of 10% of the thickest trees in the transect.

The formula for the calculation of utilization of available crown space (UAS_L):

$$UAS_L = \frac{C_L}{V_L} \times 100 \quad (\%)$$

Trunk volumes of individual tree species were determined using the volumetric tables of Petráš and Pajtík (1992).

RESULTS

Utilization of available crown space and canopy closure

The information on the basic characteristics of natural forest at the growth stage is given in Table 1. At the beginning, it is necessary to emphasize that spruce occurs only on PRP 1, because this plot is located in a part of the reserve with different bedrock (granodiorite). When the upper layer of natural forest during the last 30 years is evaluated, it is apparent that except for the first measurement in 1972, beech is a predominant species utilizing the available growth space of the natural forest all the time. Its share in the utilization of available growth space permanently increased and reached 29.41% in the upper layer in 2002. When all species are evaluated jointly, the utilization of available crown space exhibited an increasing trend and reached 58.76% in 2002. At this plot, the intermediate layer is partly

Table 2. The utilization of available growth space according to tree species and levels in the natural forest of NNR Hrončokovský Grúň in a time span of 30 years (breakdown stage) (PRP 2)

Year	Upper level		UAS_s/UAS_L	Intermediate level		UAS_s/UAS_L	Total		UAS
	species	C_{kd} (m^3)	(%)	species	C_{kd} (m^3)	(%)	species	C_{kd} (m^3)	(%)
1972	Beech	1,705.73	17.28	Beech	20.60	0.21	Beech	1,726.33	8.75
	Spruce	262.72	2.66	Spruce		0.00	Spruce	262.72	1.33
	Fir	284.56	2.88	Fir	4.12	0.04	Fir	288.68	1.46
	Ash	245.22	2.48	Ash		0.00	Ash	245.22	1.24
	Maple	175.35	1.78	Maple	2.62	0.03	Maple	178.04	0.90
	Total	2,673.58	27.08	Total	27.41	0.28	Total	2,700.99	13.68
1982	Beech	2,063.75	22.14	Beech	74.00	0.79	Beech	2,137.75	11.47
	Spruce		0.00	Spruce		0.00	Spruce		0.00
	Fir	434.07	4.66	Fir	14.85	0.16	Fir	448.92	2.41
	Ash	552.36	5.93	Ash		0.00	Ash	552.36	2.96
	Maple	300.23	3.22	Maple		0.00	Maple	300.23	1.61
	Total	3,350.41	35.95	Total	88.85	0.95	Total	3,439.26	18.45
1992	Beech	4,779.09	51.62	Beech	657.11	7.10	Beech	5,436.20	29.36
	Spruce		0.00	Spruce		0.00	Spruce		0.00
	Fir	125.43	1.35	Fir	50.12	0.54	Fir	175.55	0.95
	Ash	616.72	6.66	Ash		0.00	Ash	616.72	3.33
	Maple	267.25	2.89	Maple	57.97	0.63	Maple	325.22	1.76
	Total	5,788.49	62.52	Total	765.20	8.26	Total	6,553.69	35.39
2002	Beech	5,372.89	55.09	Beech	837.70	8.59	Beech	6,210.59	31.84
	Spruce		0.00	Spruce		0.00	Spruce		0.00
	Fir	150.13	1.54	Fir	65.41	0.67	Fir	215.54	1.10
	Ash	681.32	6.99	Ash		0.00	Ash	681.32	3.49
	Maple	294.87	3.02	Maple	41.81	0.43	Maple	336.68	1.73
	Total	6,499.21	66.64	Total	944.92	9.69	Total	7,444.13	38.16

C_{kd} – crown volume, UAS_s – utilization of the available crown space of tree species, UAS_L – utilization of the available crown space of level, UAS – total utilization of available crown space

filled by crowns as well. However, its utilization by crowns of individual species is markedly low, ranging from 2.52% to 5.29%, with the predominance of beech. Total utilization of available crown space ranges from 24.18% (in 1972) to 32.03% (in 2002).

The situation at PRP 2 (initial phase of the breakdown stage) is characterized in Table 2. In spite of the sporadic presence of spruce in the upper layer in 1972, beech is a dominant species. Other species also occur in the upper layer, particularly sycamore maple, European ash and silver fir, and their proportion varies from 1.5% to 7%. As the breakdown continued slowly through dying-off of single trees, the reaction of beech crowns is quite rapid despite its high physical age. Beech increased the total volume of its crowns from 1,705.7 m^3 in 1972 to 5,372.9 m^3 in 2002. A threefold increase in the crown volume documents the high growth vitality of this tree species. The intermediate layer of the natural forest is filled by European beech, silver fir, and sycamore maple on this plot, whereby the utilization of available growth space by these species is low as well. In spite of the heterogeneous tree species structure with different light requirements of individual species, the natural forest does not have a differentiated height structure. On the other hand, the utilization of the available growth space of natural forest by crowns is higher than in the initial phase of growth stage.

The utilization of available crown space by the crowns of individual tree species at the optimum stage (PRP 3) of natural forest Hrončokovský Grúň is documented in Table 3. In the upper layer, the space utilization by all tree species ranged from 30.41% in 1972 to 83.91% in 2002, with beech as a dominant species. The increase in the crown volume of beech between 1972 and 2002 was almost threefold. European ash is relatively strongly represented in the upper layer, with the total crown volume of 1,733.56 m^3 in 2002, representing 19.93% of the available growth space. The intermediate layer was filled by beech (disappearing after 1992), partly by fir and maple. At this developmental stage, even the lower layer of the natural forest is slightly filled by fir.

The analysis of all three developmental stages of the virgin forest in the NNR Hrončokovský Grúň confirmed that in spite of the species richness of the tree layer and a variety of ecological requirements of tree species, height differentiation is not considerable. Total utilization of available growth space was the highest at the breakdown stage, the lowest at the optimum stage.

Canopy closure level, defined as the sum of vertical projections of tree crowns onto the ground, is characterized in Table 4. As the year 2002 is evaluated, according to the developmental stages we can state that the highest value of canopy closure was recorded at the optimum stage (172.51%), the lowest at the growth stage (125.92%). The low values of canopy closure at the breakdown stage in 1972 and 1982 were probably caused by dying-off of large beech and maple trees and by deceleration of breakdown during the last 20 years. The fluctuation of this characteristic at PRP 1 (growth stage) is caused by the same mechanism, the trees of the previous generation are dying off, including fir.

Dynamics of diameter structure in natural forest

To explain the mechanisms of tree species persistence during the observation period of 30 years, we fitted diameter class numbers during 30 years to polynomials of the 3rd and 4th degree (Figs. 1 to 3). In

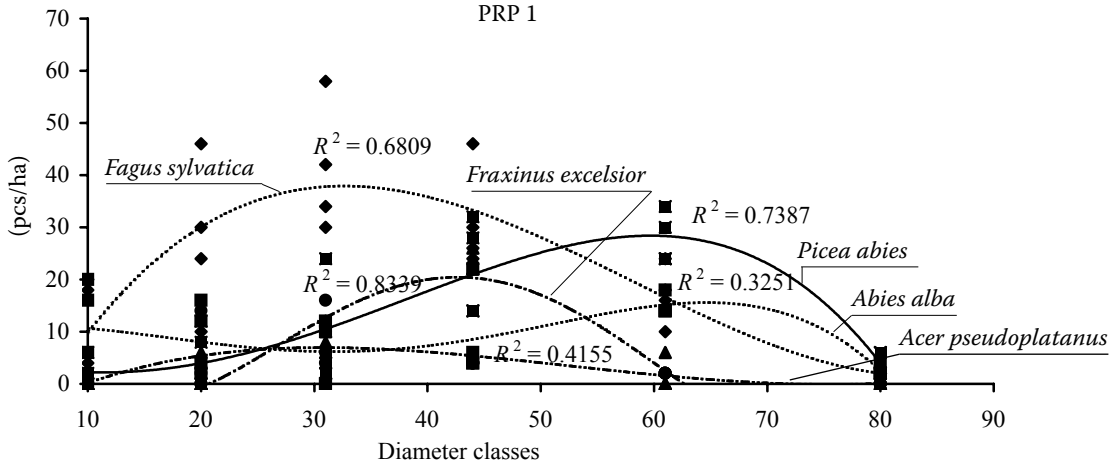

Fig. 1. Dynamics of diameter structure of natural forest NNR Hrončokovský Grúň on PRP 1 (growth stage) in time span 30 years

Table 3. The utilization of available growth space according to tree species and levels in the natural forest of NNR Hrončokovský Grúň in a time span of 30 years (optimal stage) (PRP 3)

Year	Upper level		UAS_s/UAS_L	Intermediate level		UAS_s/UAS_L	Lower level		UAS_s/UAS_L	Total		UAS
	species	C_{kd} (m^3)	(%)	species	C_{kd} (m^3)	(%)	species	C_{kd} (m^3)	(%)	species	C_{kd} (m^3)	(%)
1972	Beech	1,799.42	23.73	Beech	64.15	0.85	Beech		0.00	Beech	1,863.57	8.19
	Ash	369.64	4.87	Ash		0.00	Ash		0.00	Ash	369.64	1.62
	Fir	79.59	1.05	Fir	72.53	0.96	Fir	7.85	0.10	Fir	159.97	0.70
	Maple	57.36	0.76	Maple	16.11	0.21	Maple		0.00	Maple	73.47	0.32
	Total	2,306.01	30.41	Total	152.79	2.01	Total	7.85	0.10	Total	2,466.65	10.84
1982	Beech	3,517.50	43.41	Beech	27.24	0.34	Beech		0.00	Beech	3,544.74	14.55
	Ash	586.61	7.22	Ash		0.00	Ash		0.00	Ash	586.61	2.41
	Fir	267.36	3.29	Fir	129.17	1.59	Fir		0.00	Fir	396.53	1.63
	Maple	83.28	1.03	Maple	38.58	0.47	Maple		0.00	Maple	121.86	0.50
	Total	4,454.75	54.85	Total	194.99	2.40	Total		0.00	Total	4,649.74	19.08
1992	Beech	4,144.69	48.16	Beech	684.59	7.96	Beech		0.00	Beech	4,829.28	18.71
	Ash	751.36	8.73	Ash		0.00	Ash		0.00	Ash	751.36	2.91
	Fir	134.16	1.56	Fir	9.20	0.11	Fir	15.75	0.18	Fir	159.11	0.62
	Maple	41.87	0.49	Maple	85.36	0.99	Maple		0.00	Maple	127.23	0.49
	Total	5,072.08	58.94	Total	779.15	9.05	Total	15.75	0.18	Total	5,866.98	22.73
2002	Beech	5,192.83	59.70	Beech		0.00	Beech		0.00	Beech	5,192.83	19.90
	Ash	1,733.56	19.93	Ash		0.00	Ash		0.00	Ash	1,733.56	6.72
	Fir	155.49	1.79	Fir	31.68	0.36	Fir	46.18	0.53	Fir	233.35	0.90
	Maple	216.78	2.49	Maple	65.34	0.75	Maple		0.00	Maple	282.12	1.09
	Total	7,298.66	83.91	Total	97.02	1.12	Total	46.18	0.53	Total	7,441.86	28.83

C_{kd} – crown volume, UAS_s – utilization of the available crown space of tree species, UAS_L – utilization of the available crown space of level, UAS – total utilization of available crown space

Table 4. Canopy closure level (%) in NNR Hrončokovský Grúň in a time span of 30 years according to developmental stages

PRP	Year			
	1972	1982	1992	2002
1	103.21	115.81	107.40	125.92
2	57.49	87.68	116.96	134.22
3	94.51	137.41	125.77	172.51

PRP 1 – growth stage, PRP 2 – breakdown stage, PRP 3 – optimal stage

addition to the analysis of living trees, this procedure indirectly evaluates the variability of the dying-off of trees within individual developmental stages. In the advanced phase of the growth stage, the closest relationship (R = 0.91) was found for European ash (Fig. 1), documenting that ash is preferentially represented in the upper forest layer, is physiologically vital, which is manifested in a slow self-thinning during the period of 30 years. A high correlation (R = 0.85) was also found for Norway spruce, which is still vital because of a lower age and will die off during the optimum stage. The weakest relationship was observed in the case of silver fir (R = 0.56), which is rapidly declining in the upper layer, and its next generation in the lower layer suffers from interspecific competition and is occasionally damaged by the falling of trees of the upper layer. European beech as the bearer of the structure of this natural forest just starts to dominate from the aspect of yield and function at this stage. Because of the dying-off of trees of the upper layer and damage to the lower layer by falling trees the correlation index for beech was R = 0.82, which is significantly less than for European ash. Sycamore maple, which together with beech starts to dominate in the lower and intermediate layers, has a correlation index of R = 0.64, which is understandable concerning the behaviour of the virgin forest at this stage.

Trends of tree species persistence in the breakdown stage exhibit weaker correlations for almost all tree species (Fig. 2). Like in the optimum stage, the closest relationship was observed for European ash (R = 0.82), reflecting a low mortality of this species during the last 30 years. An equally close correlation was recorded for sycamore maple (R = 0.85) and European beech (R = 0.80). The highest mortality was recorded in silver fir, where the correlation index is the lowest, namely R = 0.71. On PRP 3, which was described as an advanced phase of the optimum stage, the correlations of the dynamics of mortality along the temporal gradient are generally less tight (Fig. 3). The closest correlation was found for sycamore maple (R = 0.88) and European ash (R = 0.83), both reaching mostly the upper layer and being physiologically vital. Beech as a dominant species and the bearer of structure has relatively high dynamics of mortality within the whole vertical profile of the natural forest and thus exhibits a moderately close relationship (R = 0.64). Silver fir, representing two generations on this plot, exhibited the lowest correlation, which is caused by the relatively fast dying-off of the older fir generation. The individuals of the subsequent generation of fir growing in the lower layer become damaged to various degrees by falling trees of the previous fir generation.

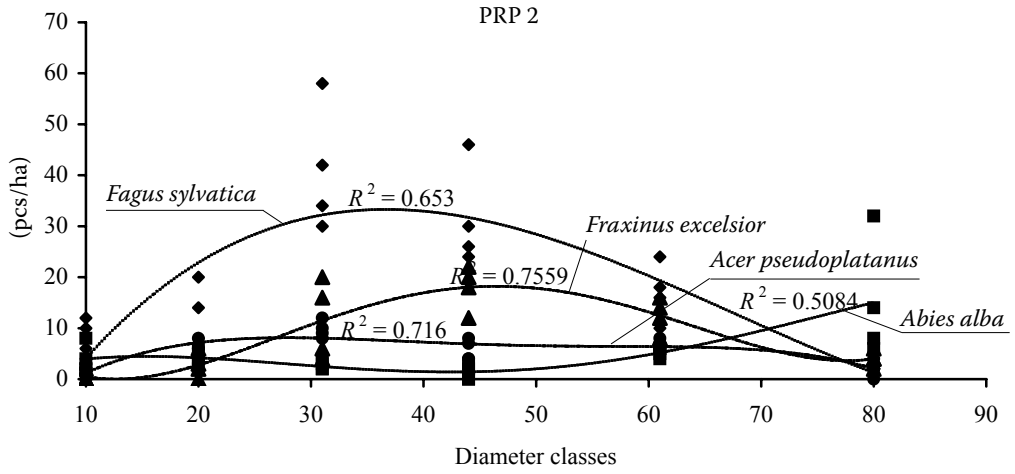

Fig. 2. Dynamics of diameter structure of natural forest NNR Hrončokovský Grúň on PRP 2 (breakdown stage) in time span 30 years

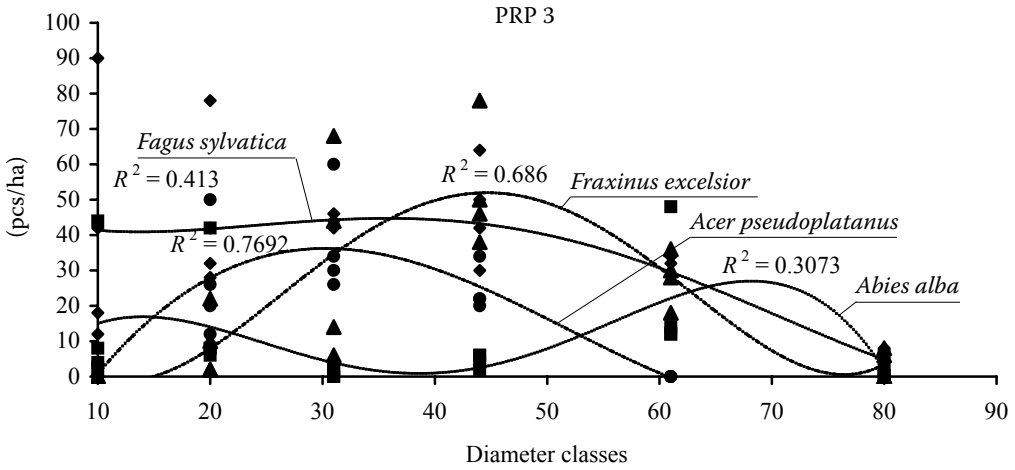

Fig. 3. Dynamics of diameter structure of natural forest NNR Hrončokovský Grúň on PRP 3 (optimum stage) in time span 30 years

Growth relationships of tree species in the natural forest

The volume growth of a tree is most influenced by the volume of the assimilatory apparatus – tree crown. To assess the growing processes of individual tree species in the primeval forest, an analysis of relationships between crown volume and trunk volume was done. The analysis of this relationship for European beech as a species forming the skeleton

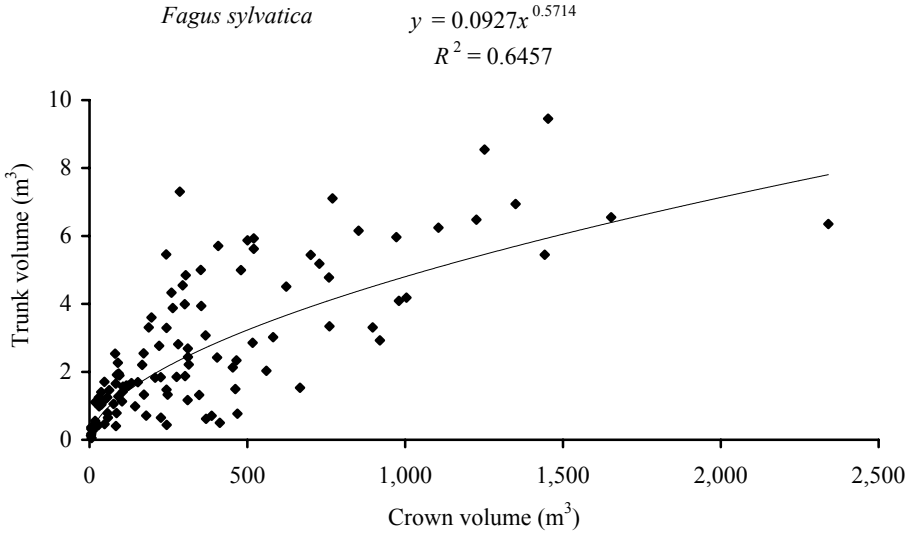

Fig. 4. The relationship between crown and trunk volume, European beech

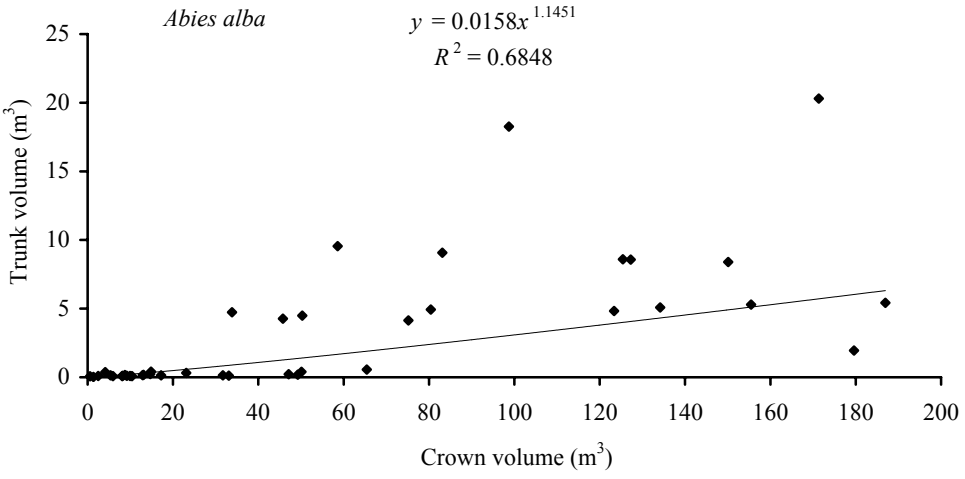

Fig. 5. The relationship between crown and trunk volume, silver fir

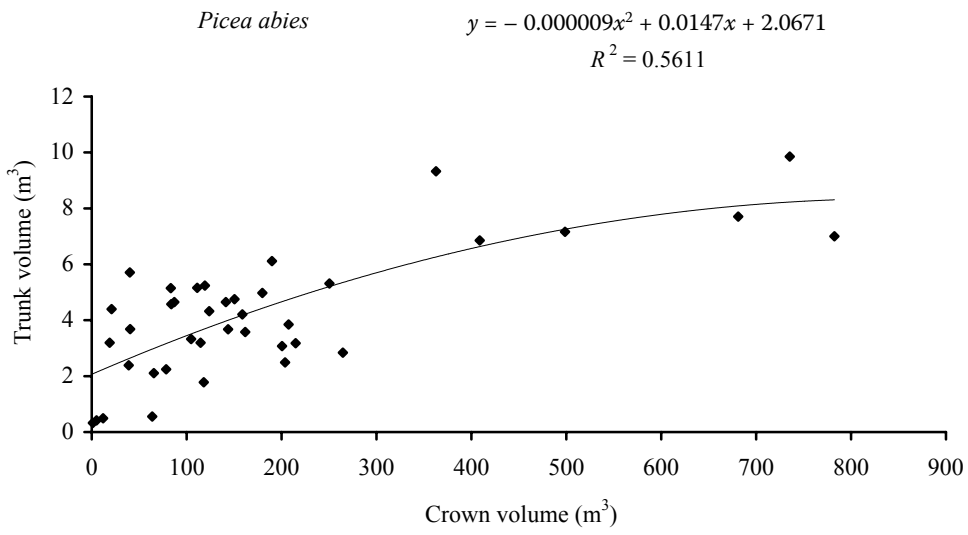

Fig. 6. The relationship between crown and trunk volume, Norway spruce

of this primeval forest confirmed a relatively close relationship R = 0.80 (Fig. 4). On the other hand, the index of determination showed that 64% of the trunk volume growth was determined by the crown volume and 36% by other factors, e.g. competition among neighbouring trees or different level of soil utilization.

Concerning silver fir as another shade-tolerant tree species of the primeval forest, a similar relationship was observed (R = 0.82) (Fig. 5). Testing these two correlation indexes did not confirm a significant difference between beech and fir. In the case of fir, the processes of stem growth and increment are similar to those of beech.

The analysis of growth relationships between crown and trunk volume in Norway spruce confirmed a close correlation, R = 0.75 and index of determination R^2 = 0.56 (Fig. 6), meaning that the volume of assimilatory apparatus contributed to trunk volume by 56%.

The analysis of this relationship for European ash, which reaches a height of 49 m in this reserve, is presented in Fig. 7. A high correlation index R = 0.79 indicates a very tight correlation and a 62% effect of assimilatory apparatus on trunk volume, whereby only 38% of trunk volume variation was caused by other factors.

A similar situation was found in sycamore maple (Fig. 8). A high index of determination R^2 = 0.71 together with a correlation coefficient of 0.84 confirmed a similar relationship like in European ash. The testing of these two correlation coefficients did not confirm any significant difference. The same effect was recorded in the analysis of determination indexes R^2 among European ash, sycamore maple and European beech.

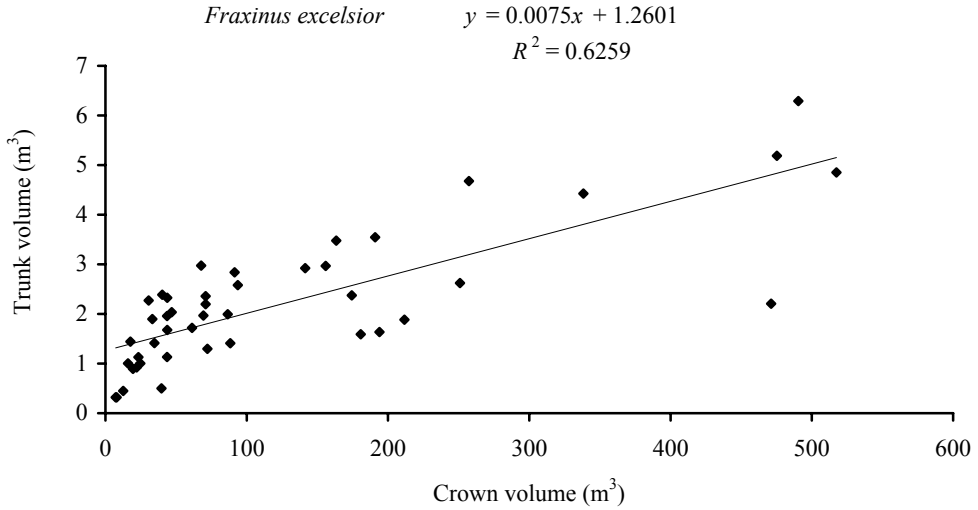

Fig. 7. The relationship between crown and trunk volume, European ash

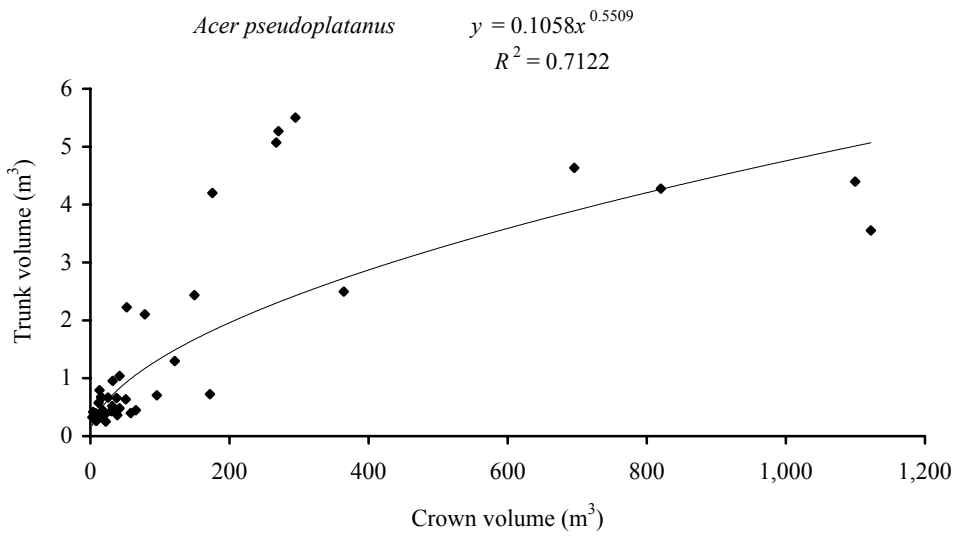

Fig. 8. The relationship between crown and trunk volume, sycamore maple

DISCUSSION AND CONCLUSION

The natural forest of the nature reserve Hrončokovský Grúň with a diverse tree species composition is a rarity among forest ecosystems of Central and Eastern Europe (Korpeľ 1989, 1995). This diversity is caused by a gradual change of bedrock on one third of the area of this natural forest. On the one hand bedrock is andesite, on the other hand it is granodiorite and siliceous diorite, whereby PRP 1 is situated just on the diorite bedrock, providing favourable growing conditions for Norway spruce. On the other hand, PRP 2 and PRP 3 are located in a part of the reserve with andesite bedrock. They are formed of plant communities associated with well aerated and nutrient-rich Cambisols, which provide optimum conditions for the growth of European ash and sycamore maple. In this reserve, ash and maple reached maximum heights that have ever been recorded within the research of any broadleaved natural forest of Slovakia (Saniga 2004). Optimum environmental conditions caused that the trunk volume growth is most affected by the capacity of their assimilatory apparatus, in spite of the fact that they are both moderately shade-tolerant tree species. In the case of these two tree species, improved soil conditions balanced the lack of sunlight in the middle and upper third of crown space. The second factor most affecting the strange correlation is their height position in the upper level. Here the crowns have almost self-standing positions. The knowledge of this problem has not been published yet. Nevertheless, the findings from research of relations between the parameters of crowns and stem volume increment on thinning plots confirm this fact (Utschig 2002). Similar relations were confirmed for fir and partly for spruce in the selection forest that represents the advanced phase of growth stage (Saniga,Vencúrik 2007). The analysis of tree number dynamics according to tree species, diameter classes and developmental stages approximated by polynomial regressions confirmed that fir dies off in the advanced phase of the growth stage and at the beginning of the optimum stage, when the second generation of beech becomes predominant. The correlation coefficient for fir documents a moderately close relationship.

The analysis of selected yield indicators of individual tree species confirmed that under favourable soil conditions, maple and ash as moderately shade-tolerant admixed species are able to maintain their position in the growing space of this natural forest, in spite of the fact that beech is a dominant species.

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Dynamika zmeny drevinovej štruktúry a charakteristík využitia rastového priestoru vo vektore času v pralese NPR Hrončokovský Grúň

ABSTRAKT: Prales v NPR Hrončokovský Grúň patrí z hľadiska drevinovej štruktúry medzi bohaté. Zastúpenie drevín smrek, jedľa, buk, jaseň štíhly, javor horský a brest ho zaraďuje medzi botanické rarity. Práca pojednáva o dynamike zmeny hrúbkovej štruktúry jednotlivých drevín ako aj o ich vybraných produkčných charakteristikách v tomto pralese. Predmetom analýzy bola hrúbková štruktúra jednotlivých drevín v jednotlivých vývojových štádiách pralesa, zisťovaná priemerkovaním v rokoch 1972, 1982, 1992 a 2002 na trvalých výskumných plochách (TVP) o výmere 71,5 × 70 m (0,5 ha). Hrúbkové početnosti stromov jednotlivých drevín, zistené v uvedených rokoch merania, boli aproximované krivkami. Cieľom uvedenej závislosti bolo posúdiť ich mortalitu, resp. vitalitu na základe tesnosti korelácie v jednotlivých vývojových štádiách pralesa. Najtesnejšia závislosť bola potvrdená v pokročilej fáze štádia dorastania, pričom najvyššiu závislosť vykazoval jaseň štíhly. Buk ako nositeľ štruktúry pralesa mal závislosť stredne tesnú. Pokročilá fáza štádia optima je charakteristická nižšími hodnotami korelačných koeficientov všetkých drevín. Rastovú vitalitu a tým menšiu mortalitu si udržiavali javor a jaseň. Buk ako nositeľ štruktúry sa vyznačuje vyššou mortalitou a tým menej tesnou koreláciou. V štádiu rozpadu sa potvrdila najväčšia mortalita pri drevine jedľa, čo potvrdzuje najnižší korelačný koeficient. Rozbor rastových a produkčných vzťahov bol vykonaný z tranzektov troch TVP, ktoré mali výmeru 10 × 71,5 m, tj. celkom 2 145 m^2. Analýza rastových vzťahov medzi objemom koruny a objemom kmeňa potvrdila vysokú korelačnú závislosť pri drevine buk a jedľa napriek tomu, že sa nachádza v celom výškovom profile pralesa. Dôvodom je ich vysoká tolerancia na svetlo a optimálne rastové podmienky. Vysoký korelačný koeficient pri drevine javor a jaseň (R = 0,82, resp. R = 0,84) svedčí o významnom vplyve asimilačného aparátu na objem kmeňa. Dôvodom je skutočnosť, že obe dreviny sa nachádzajú v porastovej úrovni a majú relatívne autonómne postavenie svojich korún. Produkčné využitie rastového priestoru pralesa potvrdilo dominanciu buka ako nositeľa štruktúry.

Kľúčové slová: prales; vývojové štádium; využitie rastového priestoru; štruktúra

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