Relation of dead wood course within the development cycle of selected virgin forests in Slovakia

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ABSTRACT: Following measurements of dead wood (20 to 40 years) at various developmental stages of the life cycle of selected virgin forests of the 1st to 7th altitudinal zone the relation of its course was derived. The dynamics and course of dead wood in the life cycle of virgin forests were best represented by a polynomial of the third degree. An analysis confirmed that virgin forests consisting of stable tree species with approximately the same physical age (Boky) showed small differences between maximal increase and decrease in necromass during the whole development cycle. Virgin forests at sites rich in nutrients consisting of several tree species with various physical age had high values of necromass during their whole development cycle. Spruce stands at the upper forest boundary also had a relatively high ratio of necromass at the advanced optimum stage.

Keywords: dead wood; development cycle; virgin forest; developmental stages

Dead wood is a sustainable basic component of natural forest. During the whole period of phylogenetic evolution, natural forests have developed a specific rich and balanced spectrum of organisms that are dependent on each other and on external and internal environment. Dead wood has become the focus of attention especially in connection with research on natural forests and reserves of biodiversity.

Scientific research on dead wood accelerated at the end of the 80's of the 20th century. The papers focused on its significance in forest ecosystems (Albrecht 1991; Köhler 1990; Schmitt 1993; Utschick 1991) and on its quantification in natural and virgin forests as well (Erdmann-Wilke 1997; Korpeľ 1989, 1995; Meyer et al. 1998; Meyer 1999; Röhrig 1991; Saniga, Schütz 2001a,b). The papers dealing with the course of dead wood within the development cycle of virgin forests have not been published so far. Stöcker (1999) made a particular trial. He tried to describe the course of necromass increase and decline within the development cycle of spruce natural forest. The attempts like this require long-term necromass observations and measurements within the virgin forest development cycle. Such values are available in the Slovak virgin forest rests where a systematic research has been carried out for 30–50 years. The research includes virgin forests from 1st to 7th altitudinal zone and it is performed by Department of Silviculture at the Faculty of Forestry in Zvolen (Korpeľ 1995; Saniga 1999a,b).

The long-term dynamic balance of forest ecosystems was retained through specific proportionality of living and dead components. A part of organic dendromass that is represented by standing and dead trees at various decay stages is also a sustained part of the integrated group. In these forests ecosystems without any anthropogenic influence in remote areas, specific and typical proportionality of volume and structure of necromass was obtained and specified. Wood necromass has a specific potential share in balance and forest ecosystem stability. Dead wood has its course of increase and decline within the development cycle similar to the living dendromass course characterised by maximum production at the optimum stage.

METHODS

RESEARCH OBJECTS

To find out the course and determination of dependence according to particular developmental stages, measurements of necromass in chosen Slovak natural forests from 1st to 7th altitudinal vegetation zone were used. These natural forests are as follows:

– National Nature Reserve Boky (tree species composition: sessile oak and Turkey oak),
– National Nature Reserve Sitno (tree species composition: beech, sycamore maple, hornbeam, ash, lime, fir),
– National Nature Reserve Havešová, Rožok, Kyjov (tree species composition: beech),
– National Nature Reserve Stužica (tree species composition: beech, fir),
– National Nature Reserve Hrončokovský grúň (tree species composition: beech, maple, ash, elm, fir, spruce),

– National Nature Reserve Badín virgin forest (tree species composition: beech, fir),
– National Nature Reserve Dobroč virgin forest (tree species composition: beech, fir, spruce),
– National Nature Reserve Poľana (tree species composition: spruce),
– National Nature Reserve Kosodrevina (tree species composition: spruce).

National Nature Reserve Boky

The reserve with an area of 176.5 ha is situated in the south-eastern part of the Kremnické Mts. on a south and south-west oriented steep slope with a gradient of 25–40°, at the altitude of 280–590 m above sea level. The average annual temperature is 7.5°C, average annual precipitation 720 mm. The parent rock is built of andesite agglomerates where different soil depth, detritus and stone field were formed by uneven weathering. Brown forest soil is a dominant soil type. At the bottom of the slope and in side terrain depressions immature soil occurs on gravel-rock detritus and in a stone field.

In the upper parts of the slope below the crest forest type group (ftg) *Corneto-Quercetum* with subgroups *CoQ carpineum, CoQ acerosum, CoQ pubescentosum* is dominant. Pubescent oak is ecologically represented by Turkey oak (*Q. cerris*) with its northernmost contiguous occurrence. In 1974, 1984 and 1994 measurements of necromass were made at particular stages of the virgin forest development cycle.

National Nature Reserve Sitno

This reserve with an area of 45.5 ha is situated at the crest and below the crest steeps of Sitno Mts. with a gradient of 25–30° (Štiavnické Mts.), 750–1,010 m a.s.l. The parent rock is built of andesite agglomerates. The soil type is Dystric Cambisol associated with Rankers of various depths formed by andesite agglomerate landslide. The average annual temperature is 6°C, average annual precipitation 850 mm. In the south and south-west facing part, which covers around 2/3 of the total reserve area, ftg *Querceto-Fagetum* with mosaic occurrence of subgroup *QF tiliosum* and ftg *Tilieto-Aceretum*. In respect to the rugged terrain in connection with sudden changes in site conditions, species composition and structure of reserve original stands are changing. In 1977, 1987 and 1998 measurements of necromass at particular stages of the virgin forest development cycle were made.

National Nature Reserve Havešová

The reserve with an area of 171.32 ha is situated in Eastern Slovakia in the Bukovské Mts. with a gradient of 25–35%, in the zone of Krosno flysch at the altitude of 500–650 m a.s.l. The soil type is brown forest mesotrophic soil, medium deep to deep, stony, slightly humic. According to the climate it belongs to a moderately warm zone with average annual precipitation 700–800 mm and average annual temperature 7°C.

Three forest type groups occur in the reserve: *Fagetum pauper* (*Dentaria bulbifera-Prenanthes purpure-nudum* type), *Fagetum typicum* (*Carex pilosa-Asperula odorata-Dentaria bulbifera-Prenanthes purpurea* type) and *Fagetum tiliosum* (*Carex pilosa-Asperula odorata-Mercurialis perennis* type and *Asperula odorata-Mercurialis perennis-Dentaria enneaphylos* type). In 1979, 1989 and 1999 measurements of necromass at particular stages of the virgin forest development cycle were made.

National Nature Reserve Rožok

It is situated in Eastern Slovakia in the Bukovské Mts. area at the altitude of 500–790 m a.s.l, mainly on the north oriented slopes with an area of 67.1 ha. Prevailing gradient of slope is 40–50%. The average annual temperature is 7°C, average annual precipitation 780 mm. The parent rock is dominantly built of sandstone, a smaller part of the area is built of argillaceous shales. Mesotrophic brown forest soil is a dominant soil type. The soil in the upper layer is sandy loam, humic, in the lower layer loamy to clay-loamy with gravel. *Fagetum pauper* forest type group with *Dentaria bulbifera nudum* as a dominant type of phytocenosis covers around 85% of the virgin forest area. In 1979, 1989 and 1999 measurements of necromass at particular stages of the virgin forest development cycle were made.

National Nature Reserve Kyjov

This virgin forest reserve with an area of 53.4 ha is situated in Eastern Slovakia in the north-west part of Vihorlat Mts. below the Kyjov summit at the altitude of 700–820 m a.s.l., on a moderate north and north-west facing slope. The average annual temperature is 6°C, average annual precipitation 750–800 mm. The parent rock is built of andesite. The soil type is brown forest soil, sandy loam soil, rich in basic nutrients, deep, moderately deep in areas below the crest, slightly acid. *Fagetum pauper* forest type group with *Dentaria bulbifera nudum* as a dominant type of phytocenosis is prevailing. In 1963, 1973, 1983 and 1993 measurements of necromass at particular stages of the virgin forest development cycle were made.

National Nature Reserve Hrončokovský grúň

It is s situated in the Poľana Mts., at the altitude of 600–950 m a.s.l. with an area of 54 ha. North-east to east slope orientation with a gradient of 30–45° is dominant.

The average annual temperature is 5°C, average annual precipitation 800–850 mm. The parent rock is built of andesite tuff agglomerate and pyroclastic andesite rocks. Unsaturated brown forest soil is a dominant soil type.

Four forest type groups occur in the reserve: *Abieto-Fagetum, Fageto-Abietum, Fageto-Aceretum* and *Fraxineto-Aceretum*. In 1972, 1982 and 1992 measurements of necromass at particular stages of the virgin forest development cycle were made.

National Nature Reserve Stužica

Stužica with its area of 659.4 ha is the largest virgin forest reserve in Slovakia and at the same time a reserve with the largest area of virgin forest in the 4th beech and 5th fir-beech forest altitudinal vegetation zone. It is situated in the Bukovské Mts., in the north-eastern part of Slovakia, at the border between the West and East Carpathian Mts. at the altitude of 650–1,220 m a.s.l.

Permanent research plots are situated at the altitude of 650–900 m a.s.l. from spring area to upper reach of Stužica river. Around 70% of the reserve area face the south and around 30% face the north; 20–50% slope. The average annual temperature is 5–6°C, average annual precipitation 850–1,000 mm. The parent rock are sandstone and taupe shales. Brown forest soil is dominant.

Fagetum typicum forest type group with *Asperula odorata-Dentaria bulbifera* as a dominant type of phytocenosis is prevailing. In 1971, 1981, 1991 and 2001 measurements of necromass at particular stages of the virgin forest development cycle were made.

National Nature Reserve Badín virgin forest

The virgin forest is situated in the Kremnické Mts. at the altitude of 700–850 m a.s.l. with total area of 30.70 ha. North to north-east exposition with a gradient of 20–40% is dominant.

The average annual temperature is 5.5–6°C; average annual precipitation is 850–900 mm. The parent rock is built of tuffs and andesite agglomerates. Saturated brown forest soil is a dominant soil type. *Fagetum typicum* (70% of the virgin forest area) is a dominant forest type group. In this part of forest four permanent research plots (PRP) are situated. In 1957, 1970, 1977, 1987 and 1997 measurements of necromass at particular stages of the virgin forest development cycle were made.

National Nature Reserve Dobroč virgin forest

The virgin forest is situated in the western part of Slovenské rudohorie Mts. at the altitude of 720–1,000 m a.s.l. The original area of 49.88 ha (in 1913) was enlarge to 101.82 ha. West exposition with a gradient of 30–50%.

The average annual temperature is 4.5–5°C; average annual precipitation is 890–960 mm. The parent rock is built of compressed granodiorites, granites and siliceous diorites.

Unsaturated brown forest soils with *Abieto-Fagetum* as a dominant forest type group (70%) where all permanent research plots are situated. *Filices-Asperula odorata-Oxalis acetosella-Lamium galeobdolon* are dominant forest types. The permanent research plots are situated on the original area of virgin forest. In 1958,1968,1978,1988 and 1998 measurements of necromass at particular stages of the virgin forest development cycle were made.

National Nature Reserve Poľana

This reserve with an area of 658.8 ha is situated at the crest and below the crest of Poľana Mts. with a gradient of 25–30° (Štiavnické Mts.), at the relatively wide range of the altitude 560–1,458 m a.s.l. The parent rock is built of pyroclastic andesite rocks and andesite agglomerate tuffs. East and west exposition is dominant. The average annual temperature is 4–4.5°C; average annual precipitation is 900–1,000 mm.

Sorbeto-Picetum forest type group with the forest type *Vaccinium myrthillus-Calamagrostis villosa-Homogyne alpina-Adenostyles alliariae* and *Acereto-Piceetum* is dominant. In these conditions three permanent research plots are situated. In 1974, 1984 and 1994 measurements of necromass at particular stages of the virgin forest development cycle were made.

National Nature Reserve Kosodrevina

Spruce stands with the virgin forest character are situated on the southern slope of Chopok Mts. at the altitude of 1,380–1,430 m a.s.l. South exposition, slope 30–35%. The average annual temperature is 1.5–2°C; average annual precipitation is 1,150–1,200 mm. The parent rock is built of crystalline rocks. The soil type is moderate humic podzolic soil. The soil is shallow to moderately deep, strongly stony, moist, moderately acid. According to forest typology a part of PRP belongs to the forest type group *Sorbeto-Piceetum* and phytocenosis type *Vaccinium myrthillus-Calamagrostis villosa-Homogyne alpina* (PRP No. 1 and 2) and *Vaccinium myrthillus-Dryopteris spinulosa asp. Dilatata-Homogyne alpina* (PRP No. 3). In 1976, 1986 and 1996 measurements of necromass at particular stages of the virgin forest development cycle were conducted.

METHODS OF EVALUATION

To determine the necromass dynamics within the life cycle of virgin forest we used determination of the whole period of the life cycle of particular virgin forests according to KORPEĽ (1995). The values of measured necromass at the particular developmental stages and years of measurement were attributed to the respective time periods within the whole period of the life cycle of individual virgin forest. Models of Slovak virgin forest by KORPEĽ (1989, 1995) were used as an example for location of necromass with the time increment of 10 years within the virgin forest development cycle. The necromass was differentiated neither according to the degree of decay nor according to the ratio of standing dead and lying wood.

The dependence of increase or decrease in dead wood on time was assessed by a set of functions. For fitting the dependence the polynomial function of the 3rd degree was used. It delivered the best coincidence with the course of necromass as well as the highest correlation coefficient.

RESULTS

National Nature Reserve Boky

The reserve has a virgin forest character. Total necromass course within its development cycle, which lasts 300 years, was approximated by a polynomial function of the 3rd degree with correlation coefficient R = 0.59. The relation provides information about gradual individual de-

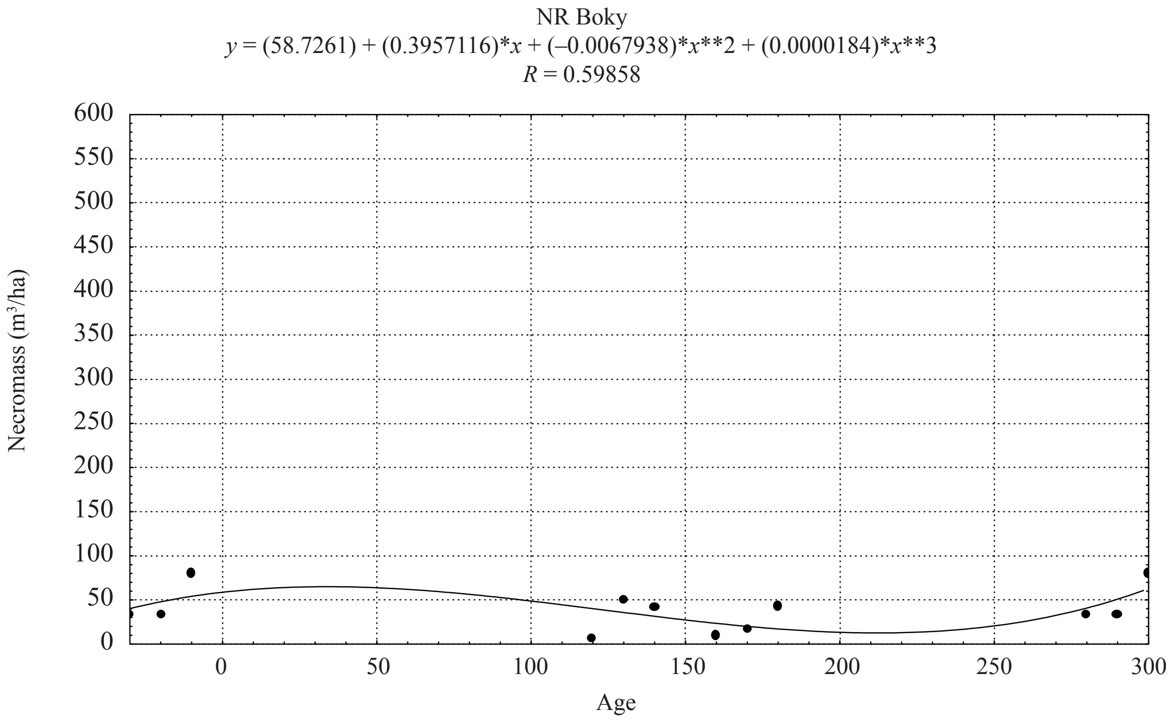

Fig. 1. The course of necromass volume within the development cycle in Boky virgin forest

cline of sessile oak trees and Turkey oak trees and about high ecological stability of virgin forest. Small-area destruction is still slowed down by Turkey oak, whose physical age is longer than that of sessile oak. It is explained by the fact that Turkey oak is not so much attacked by fungi at the end of its life as sessile oak. Because Turkey oak composition is almost the same as that of sessile oak, which dies sooner, the accumulation of necromass slows down at places that are at the destruction stage (Fig. 1).

The low ratio of necromass during the whole development cycle of virgin forest is caused by relatively low biomass values that are determined by the soil poor in nutrients (Table 1) where PRP are situated. This indicator together with gradual decline of trees that are at the dieback phase or attacked by fungi, are significant elements of continuous necromass course with its relatively low and stable values.

National Nature Reserve Sitno

The main tree species of the virgin forest life cycle on PRP No. 2 is beech together with sycamore maple. The physical age of beech and sycamore maple is nearly the same – 250 years. The necromass course is different from the previous virgin forest. The values of necromass at the

Table 1. Structure of living trees over 7cm volume in Boky virgin forest according to developmental stages

Year	PRP	Developmental stage	Tree species (m^3/ha)			Total
			oak	Turkey oak	other broadleaves	(m^3/ha)
1974	I	initial phase of optimum stage	147.25	103.06	0.21	250.52
	II	advanced phase of growing up stage	133.26	270.84	0.64	404.74
	III	advanced phase of destruction stage	180.00	108.24	6.80	295.04
		mean for development cycle	153.50	160.71	2.55	316.76
1984	I	initial phase of optimum stage	197.62	129.59	0.13	327.34
	II	advanced phase of growing up stage	159.06	284.75	1.51	445.32
	III	advanced phase of destruction stage	219.05	110.03	11.70	340.78
		mean for development cycle	191.91	174.79	4.45	371.15
1994	I	initial phase of optimum stage	195.57	144.23	0.50	340.30
	II	advanced phase of growing up stage	159.11	307.49	2.97	469.57
	III	advanced phase of destruction stage	191.57	136.48	14.97	343.02
		mean for development cycle	182.08	196.07	6.15	384.30

Table 2. Structure of living trees over 7cm volume in Sitno virgin forest according to developmental stages

Year	PRP	Developmental stage	Tree species (m^3/ha) beech	oak	maple	horn-beam	ash	lime	other broadleaves	fir	Total (m^3/ha)
1977	I	advanced phase of destruction stage	253.66	152.24	40.12	19.40	73.76	32.60	0.00	33.10	604.88
	II	initial phase of optimum stage	183.06	68.18	239.56	133.62	13.96	2.54	0.00	20.46	661.38
	III	advanced phase of growing up stage	156.74	54.08	60.82	18.74	73.76	70.14	5.96	90.12	530.36
		mean for development cycle	197.82	91.50	113.50	57.25	53.83	35.09	1.99	47.89	598.87
1987	I	advanced phase of destruction stage	262.15	119.13	46.44	18.60	47.96	34.20	0.00	31.23	559.71
	II	initial phase of optimum stage	197.51	46.12	255.48	71.41	14.09	3.13	0.00	18.74	606.48
	III	advanced phase of growing up stage	195.06	67.44	76.07	21.20	90.17	91.88	0.00	73.87	615.69
		mean for development cycle	218.24	77.56	126.00	37.07	50.74	43.07	0.00	41.28	593.96
1998	I	advanced phase of destruction stage	167.21	50.88	34.73	12.00	35.97	33.96	0.00	11.02	345.77
	II	initial phase of optimum stage	141.50	32.18	207.21	31.18	12.79	2.23	0.09	17.67	444.85
	III	advanced phase of growing up stage	183.57	56.76	76.29	18.14	99.98	95.01	3.51	83.84	617.10
		mean for development cycle	164.08	46.61	106.08	20.44	49.58	43.73	1.20	37.51	469.23

growing-up stage and at the destruction stage, which are relatively high, are very similar. A broad spectrum of the tree species composition (8 tree species), where the physical age of some species (hornbeam) is 130–150 years and of others (oak, fir) more than 300 years (Table 2), is the reason for this fact. It influences the necromass increase

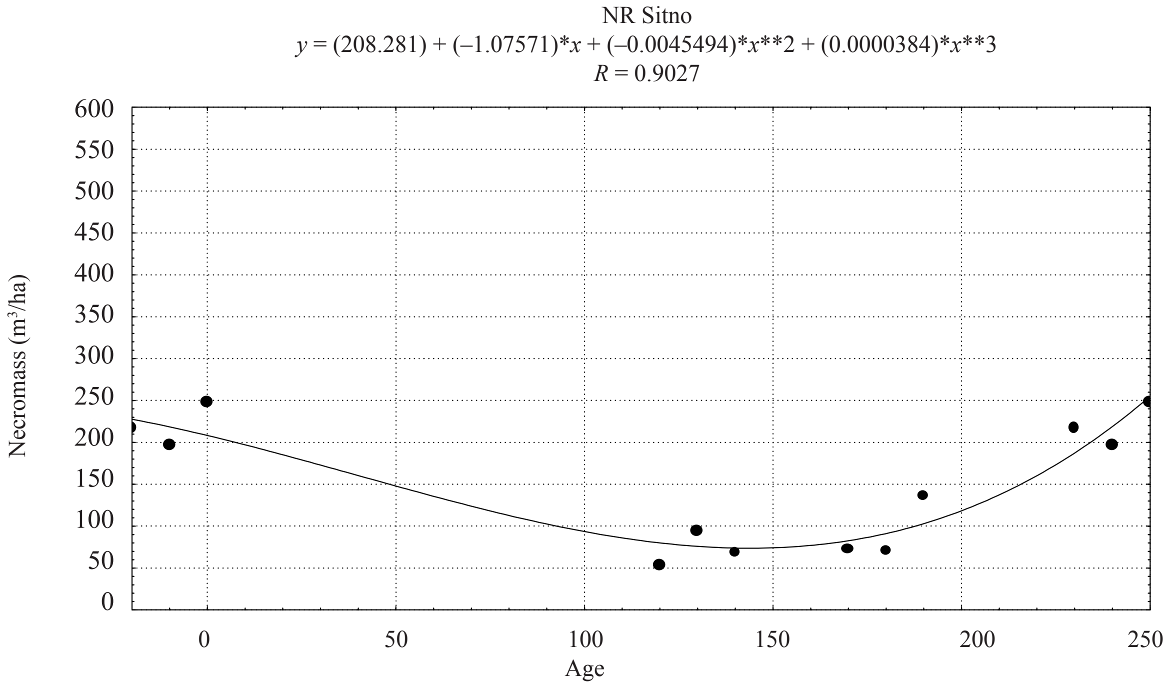

Fig. 2. The course of necromass volume within the development cycle in Sitno virgin forest

during the whole development cycle of virgin forest in such a way that drops-out occur either at the end of the destruction stage (hornbeam) or at the beginning of the growing-up stage of the second development cycle (oak, fir). We considered the fact across the virgin forest area at the beginning of the growing-up stage after oak trees dropped out, its natural seeding and advance growth took over. It is possible only if oak trees of previous generations of virgin forest can be found in the groups (0.1 ha).

Higher values of necromass are caused by a relatively high volume of biomass during the whole development cycle. The relation approximated by a polynomial function of the 3rd degree has a high value of correlation coefficient R = 0.90 (Fig. 2). On the other hand, large differences between the optimum stage and destruction stage, and between the optimum stage and growing-up stage are caused by the phase of tree species seeing out whose physical age is shorter than the physical age of beech, which together with maple determines the period of the development cycle of virgin forest. The necromass existence at the optimum stage is determined by the left-vers of fir trees whose time of decomposition is too long, 50–60 years. Dropping out of fir at the optimum stage means an increase in beech and maple growth as a response to empty growing space resulting in a higher volume increment of both tree species. On the other hand, under these ecological conditions fir regeneration is good. Fir is a continuous element almost during the whole development cycle of virgin forest. The continuity of tree species formation that are not determinant elements of the virgin forest development cycle is paradoxically given by the ecological conditions these tree species created themselves by gradual expansion of growing space or stand canopy at the advanced phase of the destruction stage.

National Nature Reserves Havešová, Rožok, Kyjov

They are beech virgin forests of the East Carpathian Mts., very similar or identical by their natural conditions. Thus, all measurements of all three reserves were collected to a common relation to better characterise necromass within the development cycle of beech virgin forest. By fitting the necromass course within the development cycle by a polynomial function of the 3rd degree relatively close relations were confirmed. Correlation coefficient R = 0.47 is significant. The course of the curve is gradual and the highest decline is between 150 and 170 years (the optimum stage). A relatively high volume of necromass at the optimum stage is connected with the fact that this stage takes a relatively short time of 30–40 years and the last remnants of the biggest beech trees that dropped out at the growing-up stage are getting to the optimum stage by their necromass. As their decomposition time is 30–35 years, they are present on the area during the whole period of this stage. These beech virgin forests are characterised by soils rich in nutrients which in turn cause shallow root systems of beech trees. In spite of their good physiological vitality and relatively considerable height of 44–46 m most beech trees are uprooted by wind at the initial phase of the optimum stage. This phenomenon causes an increase in necromass also at the optimum stage when under reference conditions the necromass does not increase (Fig. 3).

National Nature Reserve Stužica

The course of necromass within the development cycle in Stužica virgin forest is similar to that in Boky virgin forest. Correlation coefficient is R = 0.95 (Fig. 4). Besides the dominant composition of beech and fir as associated tree species (Table 3) the course of curve is characterised

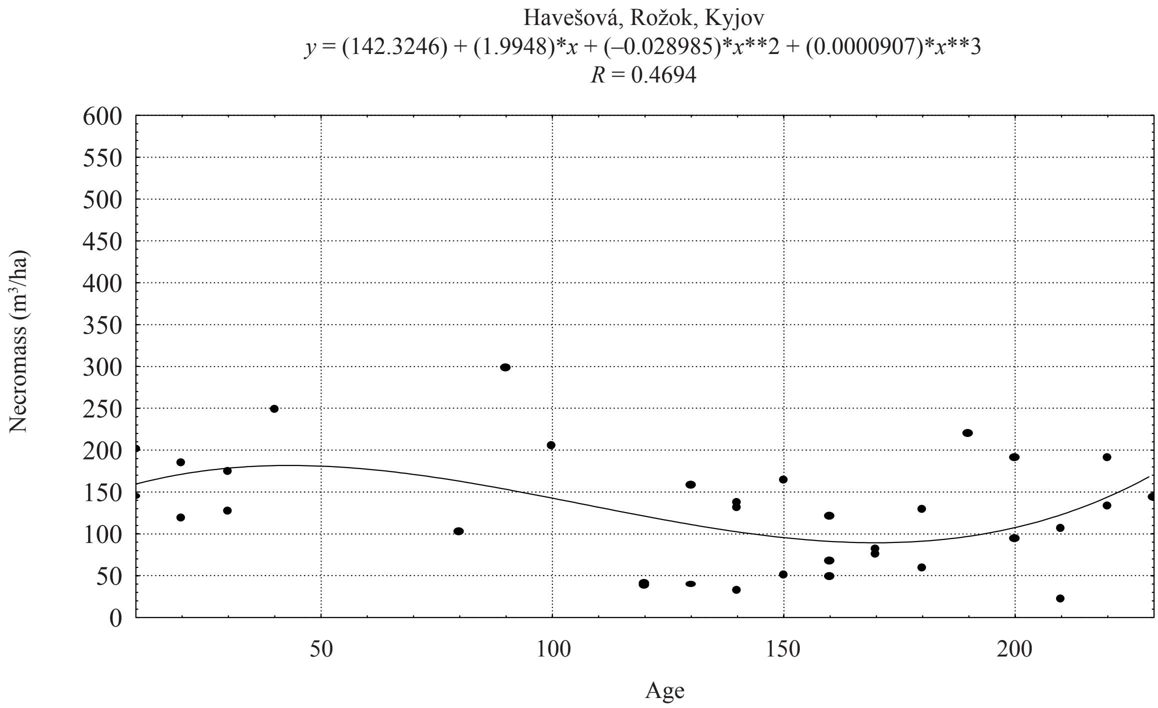

Fig. 3. The course of necromass volume within the development cycle in virgin forests Havešová, Rožok, Kyjov

Table 3. Structure of living trees over 7cm volume in Stužica virgin forest according to developmental stages

Year	PRP	Developmental stage	Tree species (m³/ha)			Total
			beech	fir	maple	(m³/ha)
1971	I	initial phase of growing up stage	558.81	2.43	5.58	563.82
	II	advanced phase of growing up stage	396.19	168.19	–	564.38
	III	initial phase of destruction stage	477.95	71.07	–	549.02
	IV	advanced phase of destruction stage	601.66	29.19	29.87	660.72
	V	optimum stage	535.44	65.52	0.87	601.83
	VI	advanced phase of growing up stage	564.49	136.74	7.67	708.90
		mean for development cycle	521.49	78.86	7.33	608.11
1981	I	initial phase of growing up stage	643.75	0.65	9.92	654.32
	II	advanced phase of growing up stage	445.66	228.72	–	674.38
	III	initial phase of destruction stage	426.63	91.36	–	517.99
	IV	advanced phase of destruction stage	616.18	19.44	19.94	655.56
	V	optimum stage	535.51	61.49	0.82	597.82
	VI	advanced phase of growing up stage	585.66	95.76	8.64	690.06
		mean for development cycle	542.23	82.90	6.56	631.69
1991	I	initial phase of growing up stage	627.19	0.86	–	628.05
	II	advanced phase of growing up stage	412.84	107.16	–	520.00
	III	initial phase of destruction stage	477.70	81.42	–	559.12
	IV	advanced phase of destruction stage	675.77	11.59	–	687.36
	V	optimum stage	512.94	22.76	–	535.70
	VI	advanced phase of growing up stage	648.52	68.14	–	716.66
		mean for development cycle	559.16	48.66	–	607.82
2001	I	initial phase of growing up stage	676.08	0.75	–	676.83
	II	advanced phase of growing up stage	435.61	45.30	–	480.91
	III	initial phase of destruction stage	505.59	86.36	–	591.95
	IV	advanced phase of destruction stage	606.26	13.11	–	619.37
	V	optimum stage	575.32	7.70	–	583.02
	VI	advanced phase of growing up stage	569.97	91.78	–	661.75
		mean for development cycle	561.47	40.83	–	602.30

by small differences between the minimum and maximum. The necromass increase at the growing-up stage is mainly caused by a decline of fir of the previous generation of the virgin forest life cycle. The optimum stage takes a very short time of 30–40 years in this reserve. Due to this fact the fir necromass, which drops out at the final phase of the growing-up stage, is maintained in the virgin forest. During the period of fir decline of 50–55 years it drifts into the initial phase of the destruction stage.

For this tree species composition we can state that there does not occur a jump increase in necromass except the fir composition higher than 10–15%. The soils poorer in nutrients in comparison with the soils in beech virgin forests of Eastern Slovakia or Badín virgin forest explain this fact. Lower nutrient contents result in deeper root systems of beech trees. These beech trees are not uprooted but they drop out in the virgin forest in consequence of their physical life. Fir is the second factor that shares in higher beech stability. Fir by its mainly single tree mixture and good root system is a significant stability element of this virgin forest (Table 3). This forest shows good signs of nutrient balance from the point of view of necromass course during the whole development cycle of virgin forest.

National Nature Reserve Badín virgin forest

More than 70% of Badín virgin forest area belongs to the forest type group *Fagetum typicum* according to typological classification. Fir is only an associated tree species in this type. Permanent research plots are situated at the boundary of this forest altitudinal zone, that means the length of development cycle is determined by beech as the main tree species of virgin forest (Table 4). The soils in Badín virgin forest were also formed on the base of andesite, very rich in nutrients similarly like in beech virgin forests of the East Carpathian Mts. These soils modify the flat shape of the beech root system. The necromass course within the development cycle is rather different from previous virgin forests. The change in shape

NR Stužica

$y = (39.1201) + (2.42746)*x + (-0.0210095)*x**2 + (0.0000501)*x**3$

$R = 0.9501$

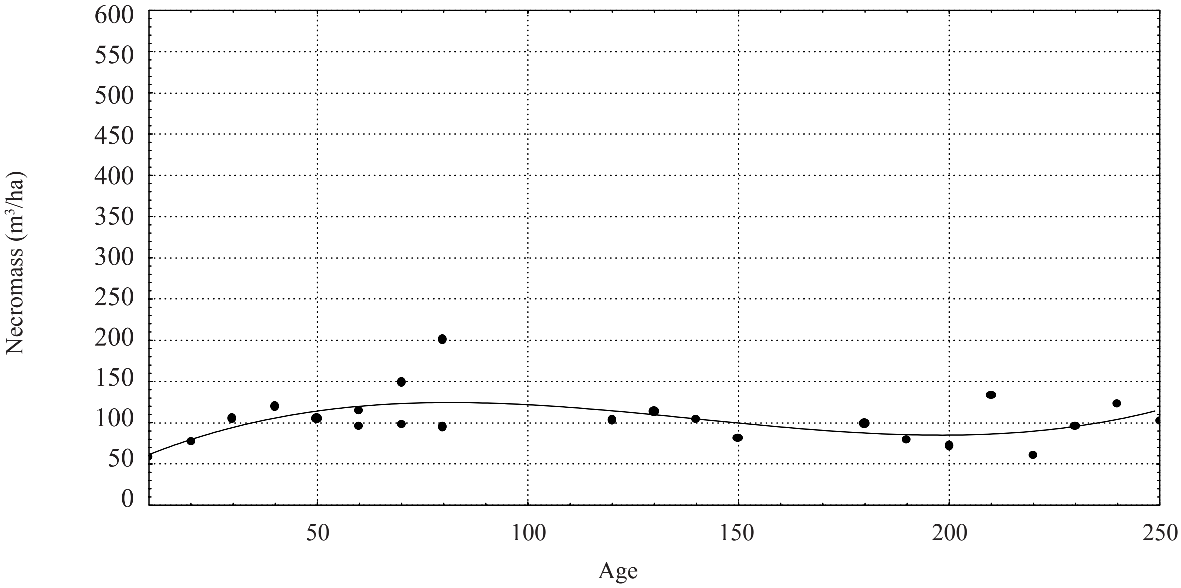

Fig. 4. The course of necromass volume within the development cycle in Stužica virgin forest

is caused by a high volume ratio of fir and its decline at the growing-up stage (Table 4) in 1970–1997 or at the beginning of the optimum stage, which takes 30–40 years. In this virgin forest such situations are common, as PRP III shows, when strong wind uprooted physiologically vital beech trees before the final phase of growing old. The

Table 4. Structure of living trees over 7cm volume in Badín virgin forest according to developmental stages

Year	PRP	Developmental stage	Tree species (m^3/ha) beech	fir	maple + elm	Total (m^3/ha)
1957	I	advanced phase of destruction stage	324.9	420.36	0	745.26
	II	mean for development cycle	324.9	420.36	0	745.26
1970	I	advanced phase of destruction stage	457.44	191.10	0	648.54
	II	advanced phase of destruction stage	463.82	317.60	0	781.42
	III	advanced phase of growing up stage	157.78	399.70	124.16	681.64
	IV	advanced phase of optimum stage	832.66	135.34	0	968.00
		mean for development cycle	477.93	260.93	31.04	769.90
1977	I	advanced phase of destruction stage	462.25	154.97	0	617.22
	II	advanced phase of destruction stage	532.47	241.47	0	773.94
	III	advanced phase of growing up stage	163.00	285.10	155.6	603.70
	IV	advanced phase of optimum stage	904.77	110.84	0	1,015.61
		mean for development cycle	515.62	198.09	38.9	752.61
1987	I	advanced phase of growing up stage	637.13	32.91	0	670.04
	II	advanced phase of destruction stage	478.82	155.75	0	634.57
	III	advanced phase of growing up stage	164.73	175.09	181.91	521.73
	IV	initial phase of destruction stage	699.63	127.94	0	827.57
		mean for development cycle	495.08	122.92	45.48	663.48
1997	I	advanced phase of growing up stage	631.52	31.70	0	663.22
	II	advanced phase of destruction stage	538.47	66.84	0	605.31
	III	advanced phase of growing up stage	205.88	142.34	153.94	502.16
	IV	initial phase of destruction stage	663.05	73.02	0	736.07
		mean for development cycle	509.73	78.48	38.48	626.69

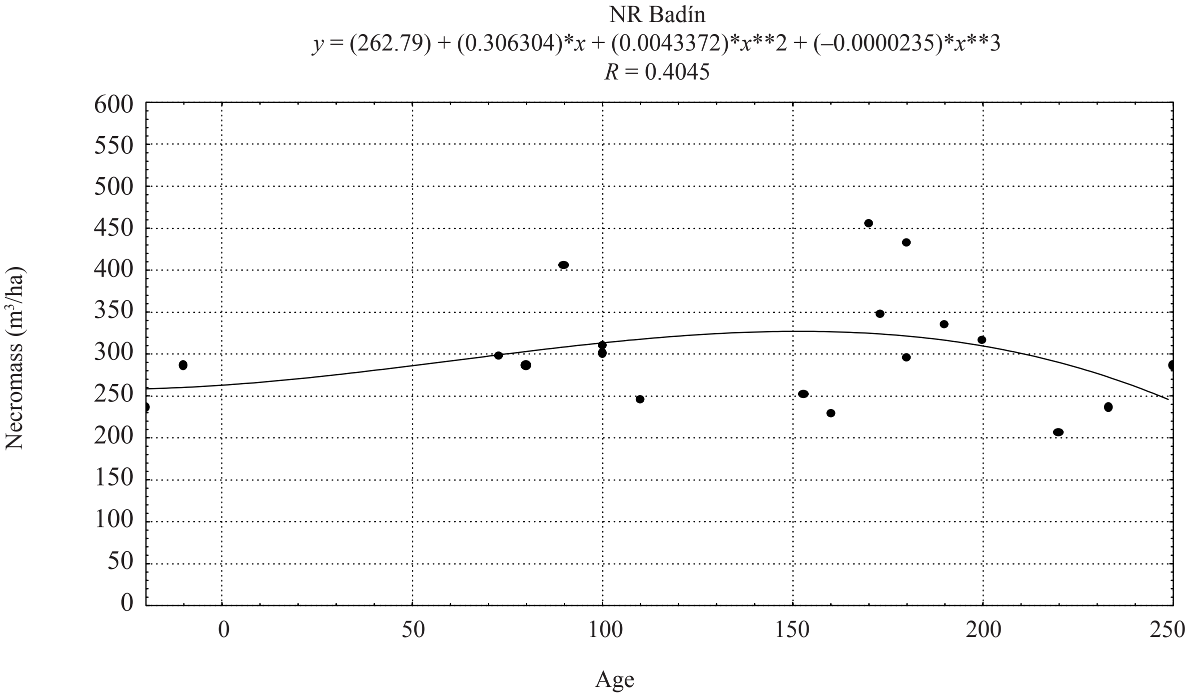

Fig. 5. The course of necromass volume within the development cycle in Badín virgin forest

polynomial function of the 3rd degree $y = 262.8 + 0.306x + 0.0043x^2 - 0.000023x^3$ has a statistically significant correlation coefficient $R = 0.40$.

The high absolute ratio of necromass in the virgin forest reflects its high volume production (Table 4). Production at the growing-up stage is conditioned by the high volume

Table 5. Structure of living trees over 7cm volume in Hrončokovský grúň virgin forest according to developmental stages

Year	PRP	Developmental stage	Tree species (m³/ha)						Total
			beech	maple	ash	elm	spruce	fir	(m³/ha)
1972	I	initial phase of growing up stage	305.20	44.20	90.20	–	247.80	151.60	839.00
	II	initial phase of destruction stage	359.60	76.80	141.20	–	50.60	473.60	1,101.80
	III	initial phase of optimum stage	289.20	135.80	418.00	–	–	252.80	1,095.80
		mean for development cycle	318.00	85.60	216.47	–	99.47	292.66	1,012.20
1982	I	initial phase of growing up stage	212.40	43.78	96.66	–	238.18	140.50	731.52
	II	initial phase of destruction stage	442.62	110.90	183.00	2.52	–	296.42	1,035.46
	III	initial phase of optimum stage	414.90	88.50	320.80	2.76	–	170.70	997.66
		mean for development cycle	356.64	81.06	200.15	1.76	79.39	202.54	921.54
1992	I	initial phase of growing up stage	218.26	29.70	86.96	–	260.46	106.52	701.90
	II	initial phase of destruction stage	442.84	127.38	217.52	–	–	154.94	942.68
	III	initial phase of optimum stage	458.90	104.40	416.14	19.96	–	116.14	1,115.54
		mean for development cycle	373.33	87.16	240.21	6.65	86.82	125.87	920.04

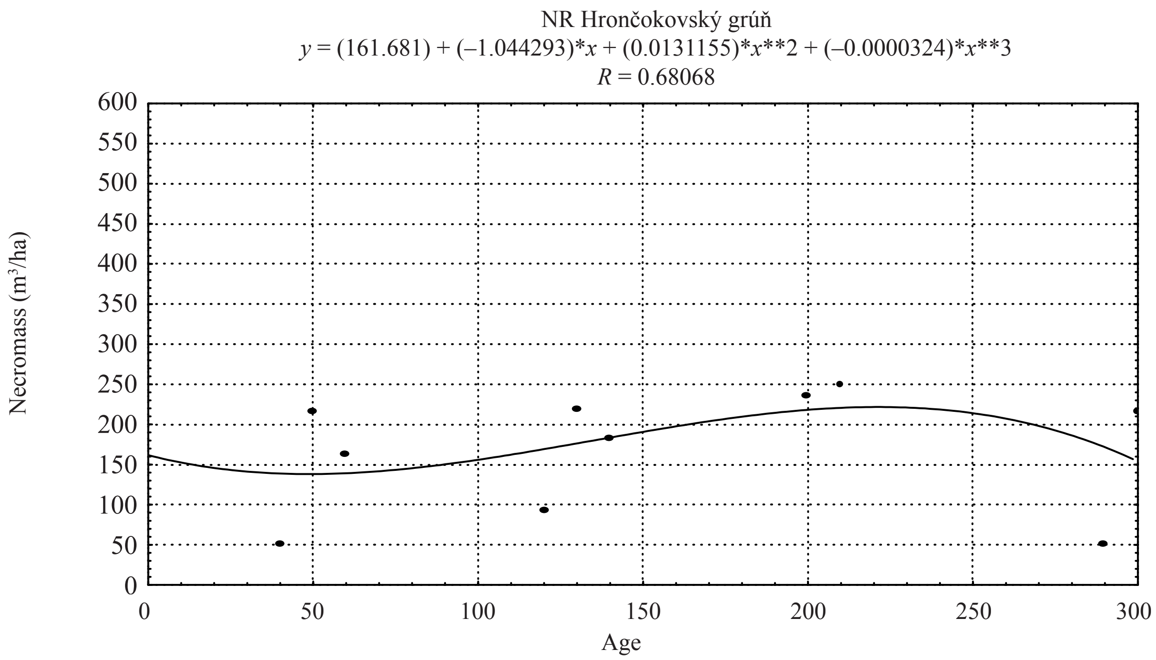

Fig. 6. The course of necromass volume within the development cycle in Hrončokovský grúň virgin forest

ratio of fir. A gradual increase in necromass at the optimum stage and at the beginning of the destruction stage is caused by a partial transfer of a part of fir necromass where the whole process of decomposition did not occur and by necromass of uprooted but still vital beech trees in consequence of their flat root systems and small crowns.

National Nature Reserve Hrončokovský grúň

The necromass course within the development cycle of virgin forest, which was determined to be 250 years, has a different character in National Nature Reserve Sitno. The correlation coefficient $R = 0.68$ is statistically significant (Fig. 6). The first information is a slow decay or a small increase in necromass during the whole development cycle. The second fact is a high volume of necromass during the whole development cycle. Approximately the same volume ratio of coniferous trees (spruce, fir) and broadleaves (Table 5) is the reason. The number of trees of particular tree species is different. The average volume of fir living trees is in the range of 15–20 m^3, beech and maple 8–12 m^3. On the basis of this fact, beech is the basic tree species of the virgin forest. Beech fills up the productive space in the virgin forest and together with sycamore maple is a determinant tree species of development cycle. Fir and spruce, whose physical age is 350–400 years, take share in the necromass at the growing-up stage and at the optimum stage, respectively, of the next development cycle. An increase in their necromass at these stages of virgin forest development cycle means the balance of necromass during the whole development cycle of this virgin forest (Table 5, Fig. 6).

The balance of necromass during the growing-up stage and its moderate increase at the optimum stage are connected with fir. Fir drops out gradually at the growing-up stage and determines the necromass value at a relatively balanced level. Because the time of fir decomposition in this reserve is relatively long (55–60 years), together with spruce it is shifting to the optimum stage. Due to this fact the course of necromass curve is rather untypical. On the contrary, it is necessary to mention that there are good conditions for germination, survival, outliving and grow-up of seedlings during the destruction stage and at the initial phase of the growing-up stage. By this, fir takes share in biomass and also in necromass volume almost in the whole development cycle of virgin forest. Hrončokovský grúň virgin forest, which represents a relatively balanced cycle of nutrients by its tree species composition, comes back through accumulation and decomposition of necromass. Due to high ecological stability and stable living mode this type of natural forest ecosystem ranks among the most balanced ecosystems in terms of production and functions.

National Nature Reserve Dobroč virgin forest

This reserve contains two tree species that by their physical age determine the period of development cycle to be 400 years. They are fir and spruce. As for the origin and course of necromass, beech has a similar role like fir in the Badín virgin forest (Table 6). The necromass course expressed by a polynomial function of the 3rd degree and correlation coefficient $R = 0.56$ is at the higher volume level than in Badín virgin forest (Fig. 7). There are two reasons for this fact. One reason is the highest biomass production of all Slovak virgin forests. The other reason for high necromass volume within the development cycle is the presence of beech, whose physical age is in the range of 220–230 years. Due to abiotic factors (wind) most beech trees drop out at their physical age of

Table 6. Structure of living trees over 7cm volume in Dobroč virgin forest according to developmental stages

Year	PRP	Developmental stage	Tree species (m^3/ha)				Total
			beech	fir	spruce	others	(m^3/ha)
1958	I	destruction stage	166.33	355.01	29.68	8.94	559.96
	II	growing up stage	105.38	442.99	245.31	0.21	793.89
	III	optimum stage	372.22	684.68	187.97	0	1,244.87
		mean for development cycle	182.20	445.58	136.88	13.70	778.36
1968	I a	initial phase of destruction stage	335.61	247.02	13.74	17.41	613.78
	I b	initial phase of growing up stage	215.84	320.94	45.74	23.12	605.64
	II a	initial phase of growing up stage	156.67	425.96	127.92	0.31	710.86
	II b	advanced phase of growing up stage	19.09	354.90	190.86	0.53	565.38
	III a	initial phase of destruction stage	67.46	256.88	425.00	16.96	766.30
	III b	advanced phase of optimum stage	318.64	295.72	460.92		1,075.28
		mean for development cycle	185.55	316.90	210.70	9.72	722.87
1978	I a	initial phase of destruction stage	324.12	201.70	10.14	17.42	553.38
	I b	initial phase of growing up stage	198.42	351.96	26.50	22.36	599.24
	II a	initial phase of growing up stage	88.08	174.48	250.36	0.16	513.08
	II b	advanced phase of growing up stage	73.06	364.36	302.32	2.04	741.78
	III a	initial phase of destruction stage	207.82	259.88	426.88	52.14	946.72
	III b	advanced phase of optimum stage	207.58	311.68	490.62		1,009.88
		mean for development cycle	183.18	277.34	251.14	15.69	727.35
1988	I a	initial phase of destruction stage	334.76	155.48	11.64	34.04	535.92
	I b	initial phase of growing up stage	255.66	295.46	68.50	7.44	627.06
	II a	initial phase of growing up stage	106.24	217.04	294.08		617.36
	II b	advanced phase of growing up stage	72.00	335.02	428.88	10.92	846.82
	III a	initial phase of destruction stage	190.14	174.46	465.02		829.62
	III b	advanced phase of optimum stage	243.16	81.12	572.86		897.14
		mean for development cycle	200.33	209.76	306.83	8.73	725.65
1998	I a	initial phase of destruction stage	354.78	196.26	8.98	40.38	600.40
	I b	initial phase of growing up stage	294.34	332.46	39.64	7.20	673.64
	II a	initial phase of growing up stage	134.88	238.44	354.24	0.18	727.74
	II b	advanced phase of growing up stage	82.28	288.34	466.84	15.66	853.12
	III a	initial phase of destruction stage	235.56	115.06	448.38	0.08	799.08
	III b	advanced phase of optimum stage	271.12	97.40	425.74	0	794.26
		mean for development cycle	228.83	211.33	290.63	10.58	741.37

150–170 years, which leads to an increase in necromass at the final phase of the growing-up stage. This trend continues at the initial phase of the optimum stage. On the contrary, by its second generation beech participates in the biomass volume at the destruction stage when the necromass created by gradual spruce and fir decay increases (Table 6). Decline and increase with maximal difference of 120–130 m^3/ha characterise the whole necromass course.

The relatively high ratio of beech and its dieback at the optimum stage create a typical necromass course in this virgin forest. Sudden decline of spruce, faster than the mass decline of fir, results in a significant increase in necromass within the whole destruction stage.

National Nature Reserve Poľana

Spruce is a determinant tree species of development cycle in this virgin forest (Table 7). The necromass course, when the period of development cycle is 350 years, as shown in Fig. 8, is fitted by a polynomial function of the 3rd degree with the correlation coefficient $R = 0.94$. Total volume of necromass, which is lower than in Dobroč virgin forest, is determined by the biomass volume that is essentially lower as a result of tree species composition and altitude (Table 7). The necromass course shows the following facts. An increase in necromass at the growing-up stage is influenced by the phase of dieback and decline of spruce trees of previous generation that die generally

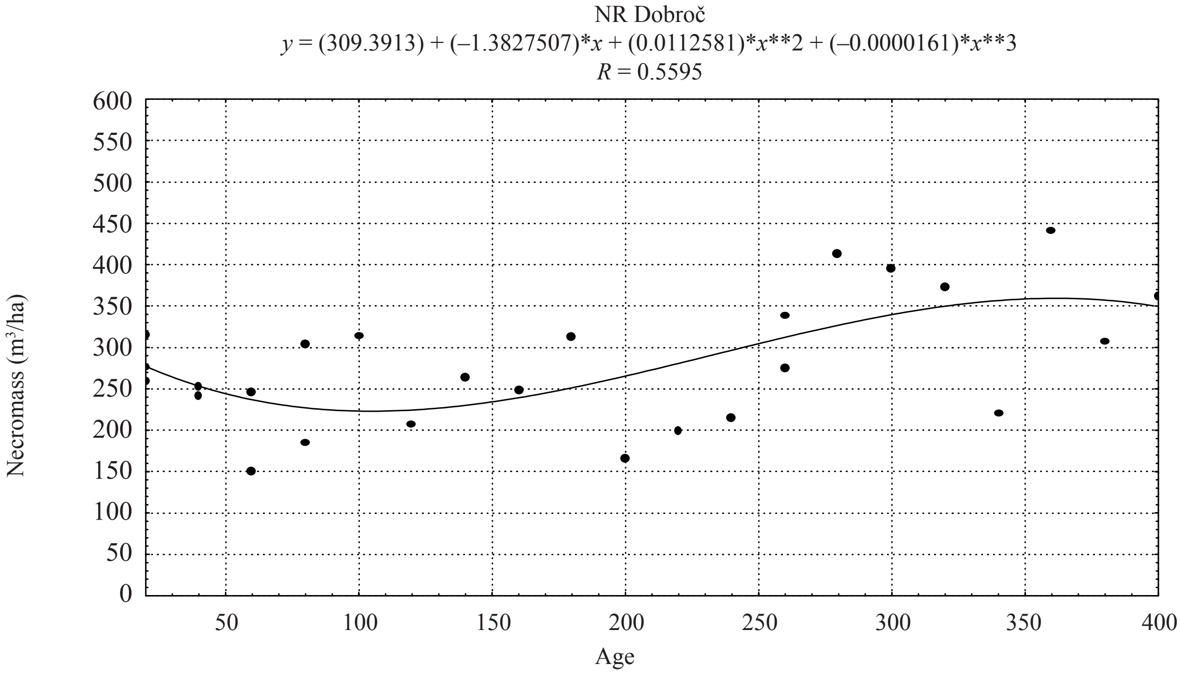

Fig. 7. The course of necromass volume within the development cycle in Dobroč virgin forest

while still standing. It is obvious because their volume is 14–16 m^3 and the time of decomposition is 50–55 years. A decline is that never reaches the zero value typical of the optimum stage. Particular trees whose volume is substituted by the growth potential of the remaining living trees also die at this stage. It is represented by the second peak of parabola till sudden destruction at the end of development cycle.

Table 7. Structure of living trees over 7cm volume in Poľana virgin forest according to developmental stages

Year	PRP	Developmental stage	Tree species (m^3/ha)		Total
			spruce	beech, maple, rowan	(m^3/ha)
1974	I	advanced phase of destruction stage	307.18	6.62	313.80
	II	advanced phase of optimum stage beginning of destruction	582.28	1.46	583.74
	III	advanced phase of growing up stage beginning of optimum	504.12	27.44	531.56
		mean for development cycle	464.52	11.84	476.37
1984	I	advanced phase of destruction stage	318.30	8.98	327.28
	II	advanced phase of optimum stage beginning of destruction	667.40	2.21	669.61
	III	advanced phase of growing up stage beginning of optimum	541.26	27.16	568.42
		mean for development cycle	508.99	12.78	521.77
1994	I	advanced phase of destruction stage	365.44	11.44	376.88
	II	advanced phase of optimum stage beginning of destruction	636.36	3.48	639.84
	III	advanced phase of growing up stage beginning of optimum	562.72	29.06	591.78
		mean for development cycle	521.51	14.66	536.17

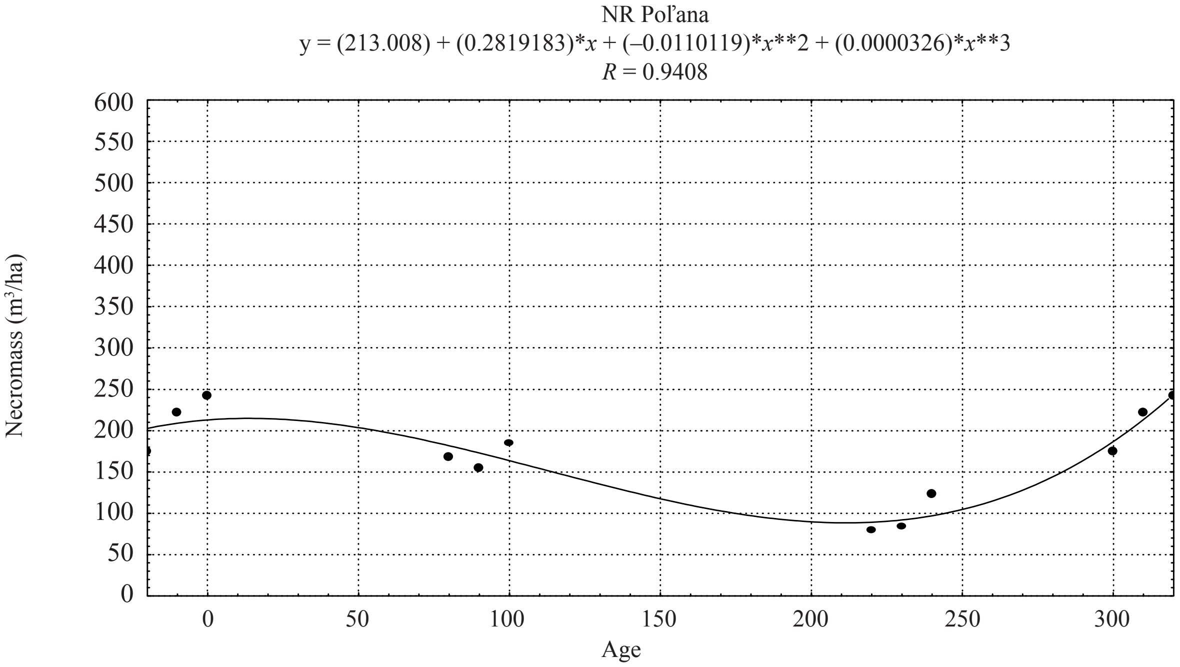

Fig. 8. The course of necromass volume within the development cycle in Poľana virgin forest

National Nature Reserve Kosodrevina

The spruce virgin forest in Kosodrevina virgin forest in the Low Tatras Mts. has a similar course of the polynomial function of the 3rd degree with correlation coefficient $R = 0.77$ (Fig. 9). The values of necromass during the development cycle are lower than in Poľana virgin forest. It is in connection with lower total volume production of biomass at the higher altitude of 1,350–1,400 m a.s.l. (Table 8). Because of area decay (wind) in this virgin forest, with increase in necromass at the initial phase of the grow-up stage, the process of necromass decomposition takes place during the whole destruction stage and at the initial phase of the growing-up stage. Also in this spruce virgin forest at the optimum stage big spruce trees sometimes drop out, which increases the necromass considerably by their dendromass, thus not reaching the zero level.

Decline or uprooting of individual spruce trees does not cause transition to the destruction stage. The virgin forest is able to fill up the growing space gradually for a long period, so the ecological conditions for the next generation growth are not suitable.

CONCLUSION

The following conclusions can be drawn on the basis of necromass course analyses in selected types of Slovak virgin forests:

Table 8. Structure of living trees over 7cm volume in Chopok-Kosodrevina virgin forest according to developmental stages

Year	PRP	Developmental stage	Tree species (m^3/ha)		Total
			spruce	rowan + beech	(m^3/ha)
1976	I	advanced phase of growing up stage	463.80	1.57	465.37
	II	advanced phase of destruction stage	515.68	6.92	522.60
	III	advanced phase of optimum stage	782.42	1.20	783.62
		mean for development cycle	587.30	3.23	590.53
1986	I	advanced phase of growing up stage	494.02	1.97	495.99
	II	advanced phase of destruction stage	476.80	7.35	484.15
	III	advanced phase of optimum stage	803.40	1.48	804.88
		mean for development cycle	591.41	3.60	595.01
1996	I	advanced phase of growing up stage	505.56	1.43	506.99
	II	advanced phase of destruction stage	441.30	8.35	449.65
	III	advanced phase of optimum stage	815.52	0.53	816.05
		mean for development cycle	587.46	3.44	590.90

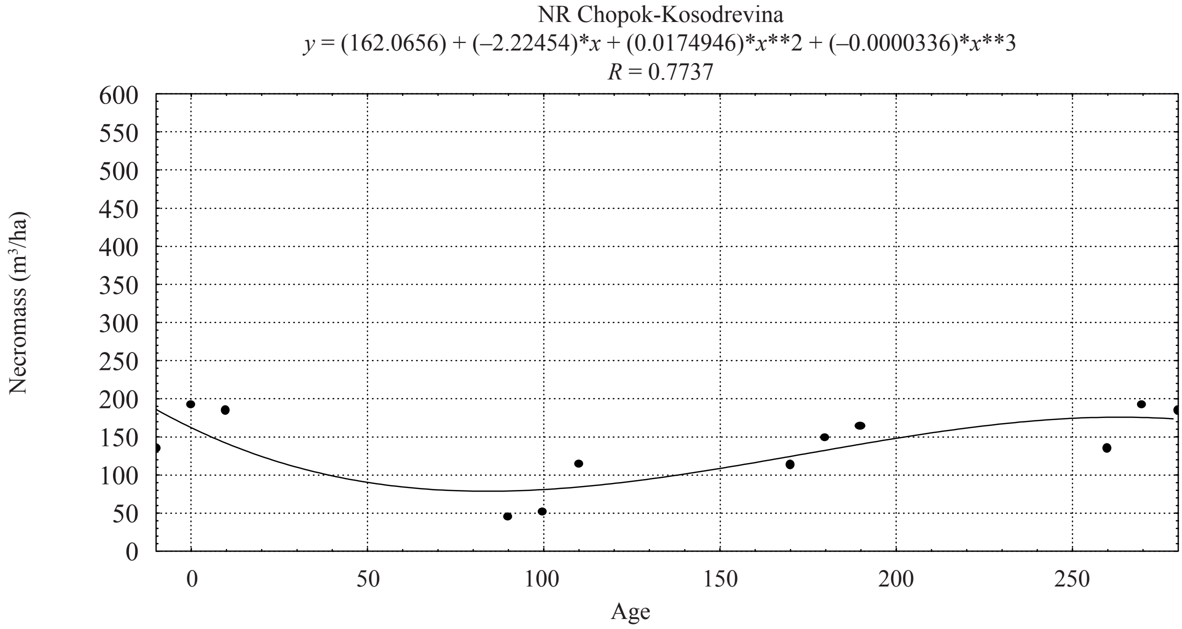

Fig. 9. The course of necromass volume within the development cycle in Chopok-Kosodrevina virgin forest

In the virgin forest consisting of two tree species with almost the same physical age and ecological requirements characterised by high stability, destruction and consistent decline of individual trees at the growing-up stage create a low gradual course of necromass with its minimum at the optimum stage.

In the virgin forest consisting of several tree species in the 3rd altitudinal vegetation zone with various length of their physical age, an increase in necromass during the development cycle is significantly higher and at the optimum stage it has essentially higher absolute values. It is caused by an increase in necromass of fir which gets to the phase of its seeing out at the optimum stage of the second development cycle of virgin forest. Tree species determining the length of development cycle (beech, sycamore maple) have approximately the same age of physical survival.

Hrončokovský grúň virgin forest has the most differentiated tree species composition (6 tree species) among the virgin forests at the boundary between 4th and 5th altitudinal vegetation zone. High values of necromass during the development cycle were obtained in this virgin forest. Similarly like in the previous virgin forest the highest increase was obtained at the optimum stage. It is especially due to fir which dies at the second development cycle of virgin forest. Beech virgin forests are very heterogeneous from the point of view of necromass course within the development cycle. The lower values of correlation coefficients confirm this fact. Relatively high values of necromass at the optimum stage are connected with beech short period and long process of decomposition. Balanced values of necromass in Stužica virgin forest and high and statistically significant correlation coefficient R = 0.95 confirm high stability and gradual beech decline during the destruction stage and the growing-up stage. The necromass increase at the optimum stage is connected with seeing out of fir from the previous development cycle of virgin forest. In Badín virgin forest high heterogeneity of necromass course within development cycles is determined by a significant fir increase, uprooting of physiologically and physically vital beech trees due to their shallow root systems and sudden gusts of wind. This phenomenon in the virgin forests in connection with climatic changes will be a part of the influence on necromass increase in the future. Dobroč virgin forest has a more balanced course of necromass and its increase at the optimum stage is mainly caused by beech decline and seldom fir decline.

Spruce virgin forest Poľana, according to site conditions, is characterised by its stability. By this, the course of necromass increase and decrease is characteristic of this virgin forest type. In spruce virgin forest Kosodrevina situated near to the upper forest limit (1,450 m a.s.l.) wind is a significant phenomenon. The necromass course is significantly changed by wind and at the optimum stage its volume increases by uprooting of physiologically vital trees.

The obtained relation should provide valid data for necromass volume determination in forests with various dominant functions.

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Závislosť priebehu mŕtveho dreva v rámci vývojového cyklu vybraných pralesov Slovenska

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ABSTRAKT: Na základe meraní mŕtveho dreva (20–40 rokov) v rôznych vývojových štádiách životného cyklu vybraných pralesov 1.–7. lesného vegetačného stupňa sa odvodil vzťah jeho priebehu. Ako najvhodnejší sa ukázal polynom tretieho stupňa, ktorý najlepšie charakterizuje dynamiku vzniku a priebehu mŕtveho dreva v životnom cykle pralesov. Analýza potvrdila, že pralesy vytvorené zo stabilných drevín, ktoré dosahujú približne rovnaký fyzický vek (Boky), majú malé rozdiely medzi maximálnym vzostupom a poklesom nekromasy v celom vývojovom cykle. Pralesy na živinovo bohatých stanovištiach tvorené viacerými drevinami odlišného fyzického veku majú vysoké hodnoty nekromasy v priebehu ich celého vývojového cyklu. Smrekové pralesy na hornej hranici lesa majú pomerne vysoký podiel nekromasy aj v pokročilom štádiu optima.

Kľúčové slová: mŕtve drevo; vývojový cyklus; prales; vývojové štádiá

Predmetom analýzy bolo overenie závislosti objemu mŕtveho dreva zisteného pri výskume vybratých pralesov Slovenska v rámci ich vývojového cyklu. Výskum sa uskutočnil v pralesoch od 1. do 7. lesného vegetačného stupňa. Jednalo sa o nasledovné pralesy: Národná prírodná rezervácia (NPR) Boky, NPR Sitno, NPR Havešová, NPR Rožok, NPR Kyjov, NPR Hrončokovský grúň, NPR Stužica, NPR Badínsky prales, NPR Dobročský prales, NPR Poľana, NPR Kosodrevina. Pre odvodenie závislosti priebehu vzniku a kumulácie mŕtveho dreva v rámci vývojového cyklu sledovaných pralesov boli využité merania za obdobie 20 až 40 rokov a bol použitý celý rad kriviek. Z nich bol vybratý polynom 3. stupňa, ktorý najlepšie kopíroval priebeh objemu mŕtveho dreva v rámci vývojového cyklu pralesa.

Na základe analýzy priebehu nekromasy vo vybraných typoch pralesov Slovenska možno vysloviť nasledovné závery:

V pralese nachádzajúcom sa v 1. lesnom vegetačnom stupni tvorenom dvoma drevinami s približne rovnakým fyzickým vekom a ekologickými nárokmi, ktorý sa vyznačuje vysokou stabilitou, rozpad a následne jednotlivé odumieranie jedincov v štádiu dorastania vytvára nízky plynulý priebeh nekromasy s minimom v štádiu optima.

V pralese tvorenom viacerými drevinami v 3. lesnom vegetačnom stupni s rôznou dĺžkou ich fyzického veku, pričom dreviny určujúce dĺžku vývojového cyklu (buk, javor horský) majú približne rovnaký vek fyzického dožívania, je nárast nekromasy v priebehu vývojového cyklu významne väčší a v štádiu optima má podstatne väčšie absolútne hodnoty, čo je spôsobené nárastom nekromasy jedle, ktorá sa dostáva do fázy svojho dožívania v druhom vývojovom cykle pralesa v štádiu optima.

Prales Hrončokovský grúň, ktorý svojou drevinovou štruktúrou (šesť drevín) patrí medzi drevinovo najpestrejšie pralesy na rozhraní 4. a 5. lesného vegetačného stupňa, má vysoké hodnoty nekromasy v celom vývojovom cykle. Podobne ako v predchádzajúcom pralese má najvyšší nárast mŕtveho dreva v štádiu optima. Tento nárast spôsobuje hlavne jedľa, ktorá odumiera v druhom vývojovom cykle pralesa. Bukové pralesy sú z pohľadu priebehu nekromasy v rámci ich vývojového cyklu významne rôznorodé, o čom svedčí aj relatívne najnižší index korelácie. Pomerne vysoké hodnoty nekromasy v štádiu optima súvisia s jeho krátkou dobou a dlhým procesom dekompozície buka. Vyrovnané hodnoty nekromasy v pralese Stužica s vysokým a štatisticky významným indexom korelácie R = 0,95 svedčia o jeho vysokej stabilite a postupnom odumieraní buka v priebehu štádia rozpadu a štádia dorastania. Nárast nekromasy v štádiu optima súvisí s dožívaním jedle z predchádzajúceho vývojového cyklu pralesa. V prípade Badínskeho pralesa je vysoká rozrôznenosť priebehu nekromasy v rámci vývojového cyklu daná okrem významného nárastu jedle vyvrátením fyziologicky a fyzicky vitálnych bukov z dôvodu ich plytkého zakorenenia a náhleho nárazového vetra. Tento fenomén v pralese bude v súvislosti s klimatickými zmenami do budúcnosti súčasťou vplyvu na nárast nekromasy. Dobročský prales má priebeh nekromasy vyrovnanejší a jej nárast v štádiu optima je spôsobený predovšetkým odumretím buka a sporadickým odumieraním predovšetkým jedle.

Smrekový prales Poľana sa vyznačuje z pohľadu svojich stanovištných podmienok stabilitou, čím sa stáva priebeh nárastu a poklesu nekromasy charakteristický pre tento typ pralesa. V smrekovom pralese Kosodrevina, ktorý sa nachádza v blízkosti hornej hranice lesa (1 450 m n. m.), sa prejavuje vplyv vetra, ktorý významne mení priebeh nekromasy a už v štádiu optima dochádza cez vyvrátenie fyziologicky vitálnych stromov ku jej nárastu.

Zistené závislosti by mali byť vodítkom pre stanovenie množstva nekromasy v lesoch s rôznou dominantnou funkciou.

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