Changes of the mixed mountain virgin forest after 70 years on a permanent plot in the Ukrainian Carpathians

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ABSTRACT: During 2004–2006, another permanent research plot (No. 12) on Pop Ivan Marmarosh Mt. in the Zakarpattya province of Ukraine was renewed, i.e. re-measured and re-analyzed. The plot was originally established in the 30's of the 20th century. The tree layer is dominated by European beech (*Fagus sylvatica* L.), with Silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* [L.] Karst.) as often associated species, and with sycamore maple (*Acer pseudoplatanus* L.) growing occasionally in small groups. After 70 years, the tree species composition partly changed. Total live timber volume increased from 529.6 to 636.3 m^3/ha. Considerable growth was recorded in beech, while the live timber volume of fir, spruce and sycamore maple did not almost change. Total number of trees (> 3 cm in dbh) increased from 737 trees/ha to 760 trees/ha. Number of beech trees increased markedly. On the contrary, fir and spruce showed a significant decrease in tree number. Interesting results emerged from the renewal of the permanent square plot (20 × 20 m), proving that beech is able to persist in the shade for more than 70 years with only minimal increment of both height and diameter.

Keywords: permanent plot; virgin forest; stand dynamics; Ukraine

In the 30's of the 20th century the young scientist Alois Zlatník and his team (Zlatník et al. 1938) established a network of permanent research plots in the present Zakarpattya province of Ukraine (Hrubý, Veska 2003). His research was aimed at the comprehension of complex relations between abiotic conditions and virgin forest types, changing in space and time. Today, more than 70 years have elapsed since the establishment of his plots. Permanent plot No. 12 was renewed in 2004.

MATERIAL AND METHODS

The main aim of this research was to record and describe changes in developmental dynamics of the forest association in research plot No. 12. The term virgin forest also includes the stands that were influenced by man, but such a disturbance has not resulted in the deflection of the natural developmental trajectory of the forest (Vrška et al. 2002). Records from the 1930's are available thanks to the above-mentioned publication (Zlatník et al. 1938), comprising methodological descriptions, maps and analytical data resulting from the research of the plots in the 1930's. Methods of our field survey strictly followed methods of Zlatník et al. (1938). The beginning of plot renewal is represented by its exact localization, i.e. localization of the position of original polygon points and so called "detailed" points, where phytosociological relevés were subsequently recorded and soil samples taken. All field works were made in 2004, except the renewal of a permanent square that was renewed in 2006.

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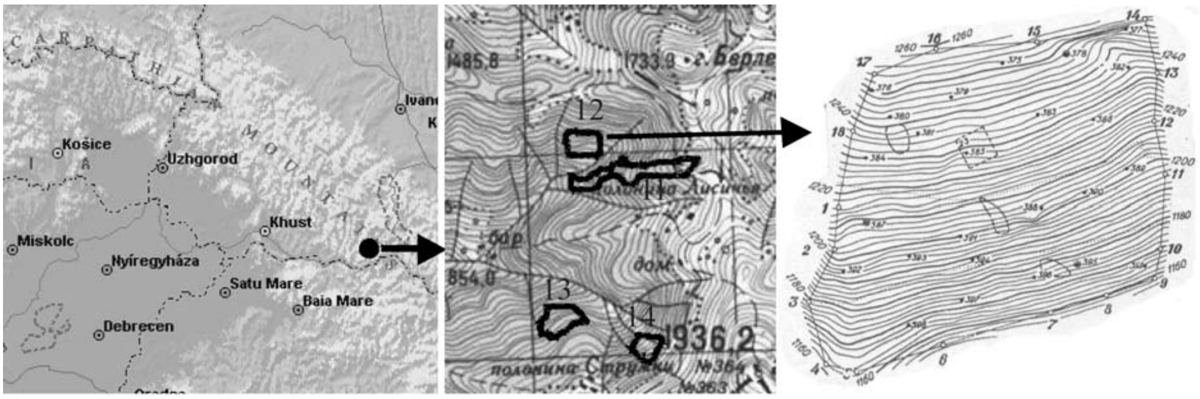

Fig. 1. Maps of Zakarpattya, the Pop Ivan plot group, and plot No. 12

The mensurational part of the study was represented by full callipering, i.e. measuring of diameter at breast height (dbh) of all trees > 3 cm in dbh. Trees with dbh < 3 cm and height > 1.3 m were counted. Diameter classes 1–3 are hereinafter referred to as "thin" diameter classes, 4–7 as "medium" and 8–13 as "thick". In the 1930's Zlatník did not map stand developmental stages and phases and did not measure deadwood volume. In 1934, in each plot a permanent square (plot 20 × 20 m) was set up so its position characterized the stand structure and tree species composition of the whole plot. The square was divided into 16 parts (16 relevés), each of them 5 × 5 m. The plan 1:50 was elaborated, depicting the position of all tree species. 72 years later, in 2006 the permanent square was exactly localized, re-measured and re-analyzed. The changes in the tree layer were described using the 5-degree scale of tree layer stratification according to Zlatník (Randuška et al. 1986).

We transformed all the scientific names of plants according to the nomenclature of Kubát (2002). Both old and new relevés were re-recorded in the MS Excel program. CANOCO for Windows 4.5 package (ter Braak, Šmilauer 2002) was used for statistical analysis. Recent use of multivariate methods has been directed at correlating vegetation with environment (Austin 2005). For better understandability of diagrams, the "species fit range" was set to 10% (ter Braak, Šmilauer 2002). Species scores were divided by standard deviation. Species cover was transformed according to van der Maarel (2005). To estimate the influence of environmental factors, the eigenvalues of the corresponding ordination axes from unconstrained (PCA) and constrained (RDA) analyses should be compared (Taggart 1994; Lepš, Šmilauer 2005).

A null hypothesis of the independence between the corresponding rows of the species data matrix and of the environmental data matrix was verified (Lepš, Šmilauer 2005). "Time" – the time span of the record from 1934 to 2006 was an environmental factor. Because the relevés create an undesirable square grid in the field, the spatial autocorrelation was reduced by means of randomization (Herben, Münzbergová 2003). The randomization was car-

Table 1**.** Characteristics of plot No. 12

Area	3.5772 ha
Ecotope	Slope 26–36°; southern aspect; altitude 1,155–1,259 m a.s.l.
Parent rock	Crystalline schist – mica schist, hydromica schist, gneiss
Soil type	Cambisol modal (ranker form)
Climate	Mean annual temperature 3.5°C; mean annual precipitation about 1,580 mm (Hrubý 2001)
Tree species	*Fagus sylvatica, Abies alba, Picea abies, Acer pseudoplatanus**
STG	(group of type of geobiocoenoses) 6 B 3 *Abieti-fageta piceae typica*

*Other woody species (*Sambucus racemosa*, *Salix caprea, Betula pendula, Ulmus glabra*) occur only scarcely

Table 2. The stand characteristics of dead trees

Characteristics/tree species	Beech	Fir	Spruce	Sycamore maple	Others	Σ
Timber volume of dead standing trees (m^3/ha) 1934	3.6	0.7	1.6	–	–	5.9
Timber volume of dead standing trees (m^3/ha) 2004	0.9	2.9	0.4	–	–	4.2
Timber volume of stubs (m^3/ha) 1934	14.6	0.2	9.1	–	–	23.9
Timber volume of stubs (m^3/ha) 2004	8.6	6.9	4.7	–	–	20.2
Timber volume of lying dead trees (m^3/ha) 2004	87.7	126.5	28.0	–	–	242.2

ried out by "rectangular spatial grid" with "reduced model" (ter Braak, Šmilauer 2002).

RESULTS AND DISCUSSION

The Pop Ivan plot group is situated in the south-eastern tip of the present Zakarpattya province of Ukraine. The study site lies under Pop Ivan Marmarosh Mountain – 1,937 m a.s.l. (Fig. 1). Characteristics of plot No. 12 are given in Table 1.

Total live timber volume increased by almost 110 m^3/ha since 1934, which represents a 20% increase. Considerable growth was recorded in beech, while the live timber volume of other tree species did not almost change. Total number of trees (dbh > 3 cm) increased by only 22 trees/ha. A considerable decrease in the number of small trees (tree individuals with dbh < 3 cm, but higher than 1.3 m) was also recorded; almost all tree species experienced decreases by approximately 50%. Total number of all small trees decreased by 456 trees/ha. Tree number and timber volume of beech, fir and spruce in diameter classes are shown in Tables 3 and 4.

Beech – the plan from 1934 shows only 3 bigger gaps in the stand of plot 12 (see Fig. 1), but canopy was disconnected at many places, which gave rise to beech regeneration clumps or compact clusters. Considerable natural regeneration is shown by a high number of small trees reaching almost 838 trees/ha, as well as by a generally lower number of beech trees belonging to medium and thick diameter classes, i.e. the trees that composing the main canopy (in the 5–9th diameter class by 15 trees/ha less than today). The thickest beech individual in the plot with 84 cm dbh reached 11.8 m^3.

After 70 years, the number of small trees decreased by almost 50%, reaching 431 trees/ha. The major part of beech regeneration has grown up and thus caused an increase in tree number in the 1st diameter class, by more than 100 trees/ha. Average diameter increment of beech regeneration amounted to about 6 cm

Table 3. Numbers of live trees in diameter classes (trees/ha) in 1934 and 2004

Tree species – year	Live small trees	1 = 3–9 cm	2 = 10–19 cm	3 = 20–29 cm	4 = 30–39 cm	5 = 40–49 cm	6 = 50–59 cm	7 = 60–69 cm	8 = 70–79 cm	9 = 80–89 cm	10 = 90–99 cm	11 = 100–109 cm	12 = 110–119 cm	13 = 120–129 cm	Σ without small trees
European beech –1934	838	233	101	41	30	35	17	10	4	1					472
European beech – 2004	431	339	100	33	32	32	28	15	5	2					586
Silver fir – 1934	53	77	62	28	12	5	2	2	2	2	1	2	1		195
Silver fir – 2004	29	25	31	31	20	6	6	3	1	1	1	1		1	126
Norway spruce – 1934	25	13	13	8	6	4	4	2	2	1	1				54
Norway spruce – 2004	6	10	5	2	3	1	4	3	1	2	1	1			31
Σ – 1934*	916	323	176	76	48	44	24	14	8	4	1	2	1	0	721
Σ – 2004*	163	374	135	66	55	39	38	20	8	5	1	1	1	1	743

*The sum of basic woody species (beech, fir and spruce). For total tree numbers of forest stand see the abstract

Table 4. Timber volume of live trees in diameter classes (m^3/ha) in 1934 and 2004

Tree species – year	1 = 3–9 cm	2 = 10–19 cm	3 = 20–29 cm	4 = 30–39 cm	5 = 40–49 cm	6 = 50–59 cm	7 = 60–69 cm	8 = 70–79 cm	9 = 80–89 cm	10 = 90–99 cm	11 = 100–109 cm	12 = 110–119 cm	13 = 120–129 cm	Σ
European beech – 1934	2.4	9.2	17.8	31.7	74.8	62.1	55.5	30.0	9.3					292.8
European beech – 2004	3.1	10.6	15.5	36.3	70.9	108.4	84.8	46.0	24.8					400.3
Silver fir – 1934	0.6	5.7	10.3	10.3	8.6	5.8	9.6	13.0	20.3	13.3	30.7	10.5		138.6
Silver fir – 2004	0.1	3.4	12.5	20.0	11.1	20.7	13.4	9.2	8.3	3.3	16.8	5.1	13.8	137.6
Norway spruce – 1934	0.1	1.5	3.3	7.5	9.2	16.0	13.6	16.4	11.0	4.1				82.7
Norway spruce – 2004	0.1	0.4	0.9	3.9	3.1	14.7	16.1	11.7	21.2	5.1	6.4			83.6
Σ – 1934*	3.1	16.4	31.4	49.5	92.6	83.9	78.7	594	40.6	17.4	30.7	10.5		514.1
Σ – 2004*	3.3	14.4	28.9	60.2	85.1	143.8	114.3	66.9	54.3	8.4	23.2	5.1	13.8	621.5

*The sum of basic woody species (beech, fir and spruce). For total timber volume of forest stand see the abstract

per 70 years. A more marked increase in tree number and especially in live timber volume occurred from the 6th diameter class (whose volume increased by 46 m^3/ha) upwards. The maximum of timber volume shifted from the 5th (in 1934) to the 6th diameter class (in 2004). In higher (i.e. thicker) diameter classes timber volume gradually decreases with the number of diameter class, due to increasing tree mortality. The most robust beech individual with 88 cm dbh reached 13.4 m^3. The results of measuring lying deadwood show that beech is there apt to windthrow during strong winds.

Fir – in 1934 the majority of fir individuals was concentrated into thin diameter classes, which is related to the ability of fir to persist in the shade with minimal increments and thus wait for favourable light conditions. Yet, a high number of firs in thin diameter classes is probably caused also by abundant fir natural regeneration in years or decades preceding the year 1934. From the 6th diameter class upwards numbers of fir trees were almost equal and did not exceed 3 trees/ha. The maximum of timber volume was concentrated in thick diameter classes thanks to a high volume of individual stems belonging to these diameter classes – the most massive fir in the plot reached 112 cm dbh and 18.8 m^3 of timber volume.

In 2004 the number of small fir trees and individuals from the 1st and 2nd diameter class was decreased by approximately 50%, analogously timber volume in these diameter classes decreased. A decrease in the fir number in thin diameter class was caused mostly by natural mortality. Only few "waiting" firs finally saw canopy openings and subsequently experienced fast increment due to increased light. Generally, the distribution of timber volume is uneven. In 2004 the most robust fir in the plot had 127 cm dbh, 44 m of height and more than 25 m^3 of timber volume.

Spruce – in 1934 the number of small spruce trees amounted to 25 trees/ha. Spruce regenerated mainly on the mineral soil – predominantly on windthrow mounds and pits. Individual spruce regeneration emerged where the layer of beech litter had been interrupted. In thick diameter classes spruce was represented, similarly like fir, only by a few trees per hectare. The most massive spruce had 90 cm dbh and 14.7 m^3 of timber volume.

In 2004 the number of small trees decreased markedly (even by 75%). Thin as well medium diameter classes experienced an evident decrease in tree number. The number of trees of thick diameter classes did not almost change in comparison with 1934. The distribution of timber volume is determined by the volume and number of stems, which is evident e.g. in the 9th diameter class, where timber volume increased to almost 100% of the previous volume (in 1934), though the number of trees in this class is only 1 stem/ha higher than in 1934. The most massive spruce in the plot was represented by a 46 m high individual with 108 cm dbh and 23 m^3 of timber volume. By measuring deadwood, spruce was found to be the species most susceptible to windthrows in the plot (despite its only 13% proportion).

Sycamore maple – the total number of trees with dbh > 3 cm did not practically change. In 1934

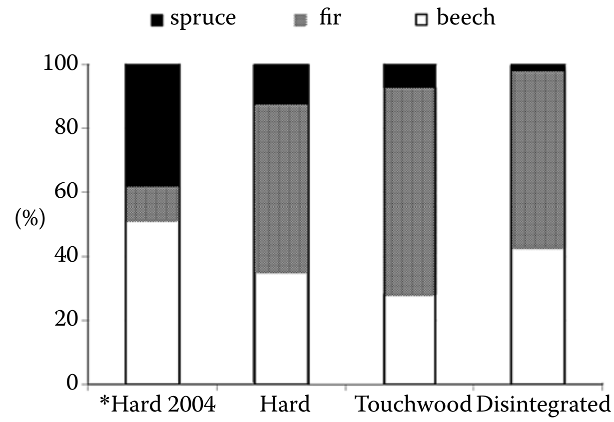

Fig. 2. Proportions of tree species in categories of lying dead trees – categories according to Vrška et al. (2002)

*The category hard 2004 comprises stems uprooted by the windstorm on July 10, 2004

sycamore maple was abundant in medium and thick diameter classes, while after 70 years it is numerous in thin diameter classes. The most massive sycamore maple had 104 cm dbh and 20.7 m^3 of timber volume in 1934. This particular tree has been so far the most massive broad-leaved tree ever measured in the plot.

Regeneration and growing up – regeneration of woody species corresponds with their ecological requirements. Only beech is able to cover larger areas in compact mass, using gaps created e.g. by the fall of individual mature trees or by windstorm-induced windthrows. Interesting results emerged from the analysis of square part No. 16, where two beeches persisted in the shade for more than 70 years with only minimal yearly increments of both height and diameter (some annual increments had even only 60 μm in dbh). This observation corresponds with findings of Svátek (2006), who found that some suppressed beech trees had not increased their girth by 0.1 mm during two years. Closset-Kopp et al. (2006) recorded the age of 135 years for beech that was 7.5 m high. Fir regeneration usually occurs only by means of individuals, at few places also in small groups among the beech regeneration. Spruce regenerates noticeably only on windthrow mounds. Our observation also discovered another way of preparation of places suitable for regeneration of conifers. In November 2005 there was observed a young bear searching for beech mast by disrupting the originally compact layer of beech litter, leaving behind pawed spots of about 1 m^2. Presumably the bear thus facilitated the germination of conifer seeds by helping them to get to the mineral soil. Regeneration of sycamore maple also bears specific features. Although sycamore maple produces a considerable amount of seeds each year, its seedlings generally have only a slight chance to survive. Sycamore seedlings survive only when they germinate in open spaces (canopy openings) where they have favourable light conditions and are able to gain and maintain height advantage over beech. To reach the main tree layer, they have to keep this height advantage permanently. Canopy openings with suitable light conditions occur usually as a consequence of destructive winds. At such places, sycamore maple is able to create small groups; e.g. a group in permanent square No. 23 probably originated in that way. Therefore the presence of sycamore maple in the studied forest is probably dependent on disturbances caused by extreme abiotic factors.

Game pressure (damage by deer) is generally considered as the crucial factor of successful natural regeneration in protected virgin forests in the Czech Republic. As Průša (2001) stated, in the most famous virgin forest reserves in the Czech Republic – Boubínský prales and Žofínský prales – this fact was proved by fence protection. Concerning the game damage, Ukrainian virgin forests have a great advantage over forests in the Czech Republic, thanks to low numbers of game being restricted not only by the presence of big carnivores but also by economic circumstances in Ukraine. On the other

Table 5. Developmental stages and phases

Developmental stages and phases	Area in hectares	% of total area
Stages of growth – selection phases	0.9836	27.5
Stages of growth	0.6976	19.5
Stages of growth – expiration phases	0.1180	3.3
Stages of optimum	0.2504	7.0
Stages of optimum – terminal phases	0.2396	6.7
Stages of disintegration – regeneration phases	1.2880	36.0
Total	3.5772	100

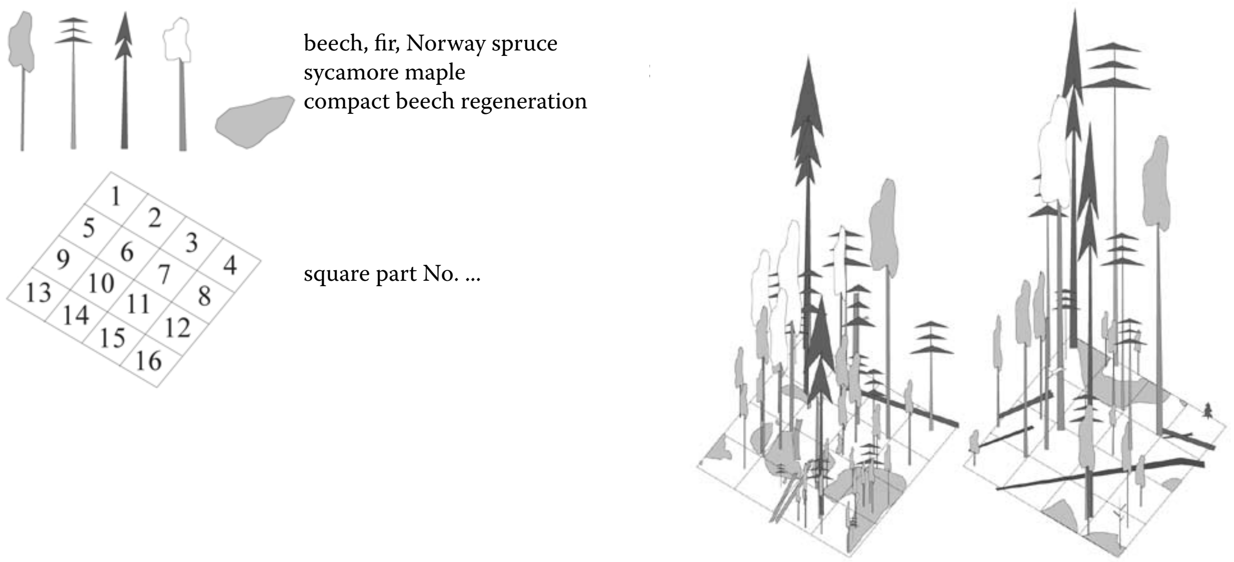

Fig. 3. Permanent square No. 23 (the situation in 1934 is on the left, in 2006 on the right)

hand, Ukrainian virgin forests (especially those lying near pastures or those being crossed by paths) are still severely endangered by grazing, still being practised in forests.

Dying of trees – measuring of deadwood revealed that beech was prone to windthrow. Uprooted beeches usually formed small groups. Decay of beech wood is very fast, which can be proved by the fallen beech with a hard compact stem in 1934, but completely decayed in 2004. Firs usually died as standing trees, most of them belonged to thin diameter classes. The number of fir snags with dbh > 80 cm is almost the same as the number of live firs of similar dbh. Fir is the most resistant to windstorm in the plot. On the contrary, spruce seems to be the species most susceptible to wind damage. Insect damage of spruce is, with respect to the small proportion of spruce in the plot, rather exceptional. Fallen fir and spruce stems decay much more slowly than beech stems. This fact is illustrated by the highest proportion of lying fir stems being in the category "touchwood" (see Fig. 2). The ratio of the total volume of dead trees to live trees is perhaps 1:2. It corresponds with the ratio that was determined by Saniga and Schütz (2002) for the stage of disintegration in a Slovakian mixed mountain virgin forest. The main characteristics of deadwood are shown in Table 2.

Development of mixed spruce-fir-beech forest – although the growth conditions of the crystalline Eastern Carpathians are fairly different from the conditions of Slovakian Carpathian virgin forests (e.g. Badínsky prales, Dobročský prales), the virgin forest mensurational characteristics of the 6th altitudinal vegetation zone described by Korpeľ (1989) are quite similar in both areas. The development cycle of a mixed spruce-fir-beech forest is very complex. All 3 tree species have their own particularities; the main one is the maximum physical age of the species. Thus typically during 1 generation of fir (or possibly spruce) 1.5–2 generations of beech rotate.

In 1934 the stage of disintegration probably predominated in the plot, because total timber volume was rather low and natural regeneration was abundant. Nowadays the stage of growth (if we summarize its phases) and stage of disintegration cover the largest area (see Table 5), which corresponds with a marked increase in beech timber volume in medium and thick diameter classes. According to Korpeľ's (1989) approach, the stand is in a developmental phase in which the main part of the area is predominated by the regenerated 2nd generation of beech. That seemingly gives an impression that beech has expanded in the studied area and that fir and spruce have been suppressed by beech. The Korpeľs definition (Korpeľ 1989) further describes the abundance of trees belonging to thin and thick diameter classes on plots larger than 2 ha, while trees of medium diameter classes should be present in a smaller number. This is partly different from the actual state of plot No. 12, in which all tree species are represented by only a few individuals of thick diameter class per hectare, while trees of medium diameter classes represent, especially in the case of beech, a considerable amount of timber volume. Although the plot area exceeds 3.5 ha, this difference can be caused by the presence of the stage of growth on more than 50% of the plot (if we summarize its phases) and by the presence of the stage of disin-

Table 6. Changes in live tree numbers in individual parts of the permanent square

Layer	Year	Beech	Fir	Spruce	Sycamore maple	Total
Layer I–II	1934	1^{3}	–	$2^{1,5}$	–	3
	2006	1^{3}	1^{2}	$2^{1,15}$	1^{10}	5
Layer III	1934	1^{10}	$3^{2,6}$	1^{15}	$5^{6,9,10,11}$	10
	2006	1^{13}	$2^{1,2}$	–	–	3
Layer IV	1934	$22^{5,7,8,9,11,12,13,15,16}$	$9^{1,4,7,12,14,15,16}$	–	–	31
	2006	$10^{2,6,7,9,12,13,16}$	$3^{1,7,15}$	1^{4}	1^{10}	15
Layer V	1934	$137^{1,2,4,5,6,7,8,9,10,11,12,13,14,15,16}$	$3^{2,6,12}$	$4^{10,16}$	–	144
	2006	$131^{1,2.3,5,6,8,10,11,12,15,16}$	$23^{1,3,6,7,8,9,12,15,16}$	2^{2}	$4^{1,4,10}$	160
Total	1934	161	15	7	5	188
	2006	143	29	5	6	182

Individuals higher than 1.3 m and thicker than 3 cm in dbh were included in layer IV. Large figures show the number of trees, small figures show No. of the part of the permanent square where trees were found

tegration – regeneration phase on 36% of the plot area (Table 5).

In the years (or decades) to come total timber volume of the stand can be expected to gradually increase, thanks to the absence of anthropogenic or abnormal abiotic impacts. However, its increase will not probably be pronounced, due to beech dominance. Fir timber volume could increase possibly only thanks to the 6th diameter class, which is the only one containing a higher number of fir trees.

Changes in the tree layer of permanent square No. 23 – after 72 years, the number of trees higher than 1.3 m and with dbh > 3 cm in the permanent square decreased from 44 (24 beeches, 12 firs, 5 sycamore maples, and 3 spruces) to 23 (12 beeches, 6 firs, 3 spruces, and 2 sycamore maples). The area of compact advanced beech regeneration also decreased markedly. The spatial stand structure became much more simplified (see Fig. 3). Numbers of trees belonging to the particular square parts are given in Table 6.

In 2006 the height of the main layer (II) was increased by a few meters in comparison with 1934. One spruce disappeared from square part No. 5 due to wind. Very intensive height increments were observed in trees that started their growth thanks to better light conditions (from 16 to 25 cm/year) and reached layer I or II of forest stand after 72 years. On the contrary, the trees that persisted in the upper or main layer (one spruce and beech) intensively increased mostly their diameter increment rather than height increment. Sycamore maple, the originally dominant species of layer III, is today absent in this layer. The number of trees in layer IV also decreased. 13 beeches and 3 firs (out of the 31 original trees) probably died and only 7 beeches, 1 spruce, and 2 firs advanced to this layer. In 1934 the compact natural regeneration of beech in layer V covered almost one quarter of the square. Today the compact natural regeneration of beech covers ⅛ of the square. Numbers of individuals in this layer probably went through considerable changes during 70 years, because for example numbers of seedlings naturally fluctuate between years.

Changes in the herb layer of permanent square No. 23 – PCA scatterplot (Fig. 4) indicates distinct differences between old and new relevés; both groups are approximately separated by the 2nd (vertical) axis. It is obvious that species situated on the left are correlated with the presence of species occurring in 1934, while species on the right are correlated with the presence of species occurring in 2006. It is interesting that in 1934 more fitted species occurred and the vegetation composition of the whole permanent square was richer and more heterogeneous. The basic characteristics of principal component analysis (PCA) are summarized in Table 7. The first two PCA axes (principal components) explained 52.1% of variability in the species data. "Time" as a supplementary variable was chosen to demonstrate the localization of relevés and species in temporal change. Because time represents a supplementary variable, environmental data are not the decisive factor affecting the localization of relevés (Lepš, Šmilauer 2005), however, the arrows representing environmental

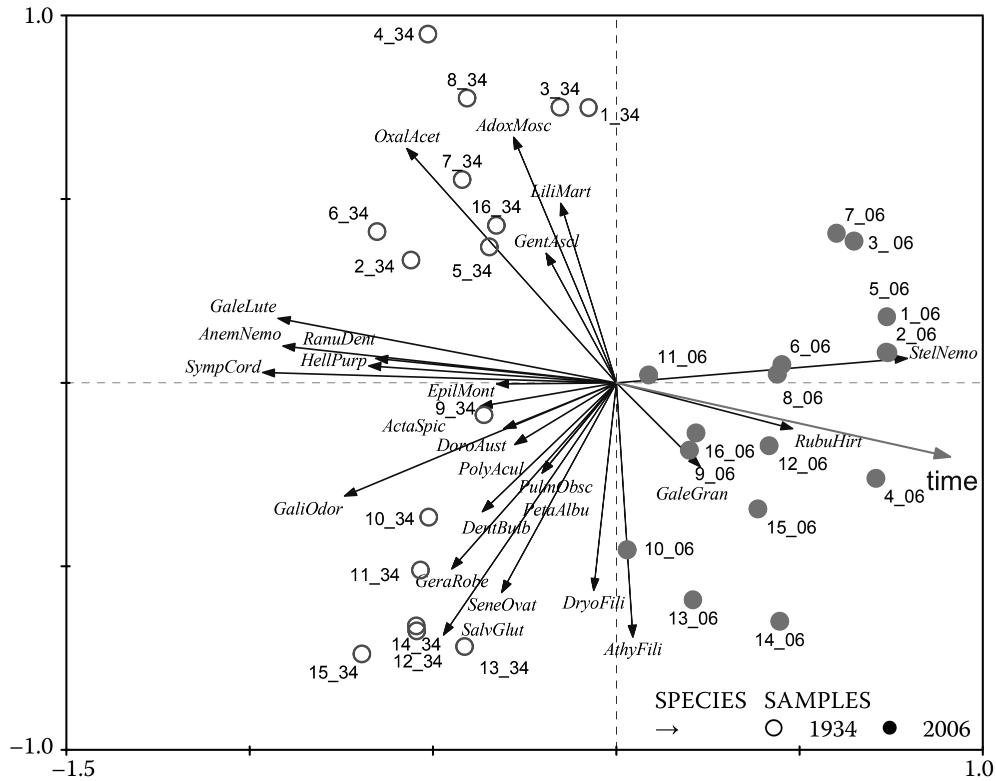

Fig. 4. PCA with 16 old (open circles) and 16 new (solid circles) relevés. The difference between relevés is obvious; they are separated by the 2nd axis. Old relevés are on the left, new relevés on the right. The species fit range is 10%. Supplementary factor "time" shows the spatial localization of relevés in temporal change

data – supplementary variables (time) show the main direction of temporal change in relation to the relevé localization.

RDA_{time} scatterplot (Fig. 5) reflects the overall vegetation change over the time period. Increased species are on the left, decreased species on the

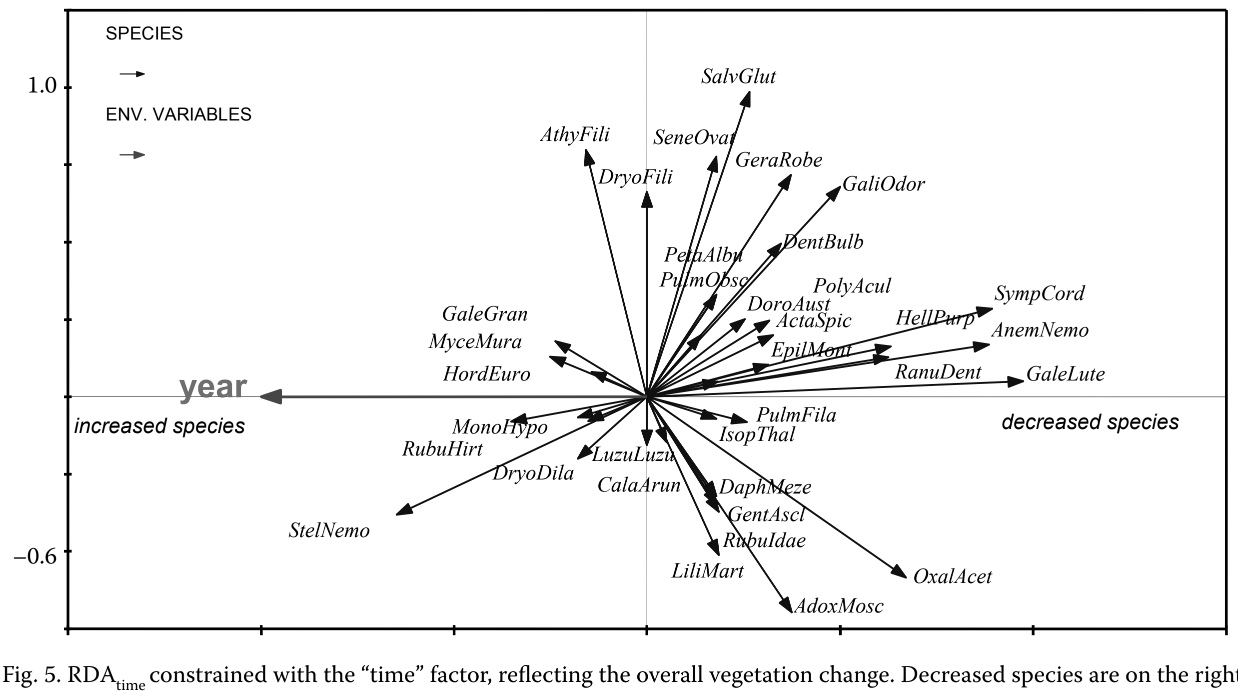

Fig. 5. RDA_{time} constrained with the "time" factor, reflecting the overall vegetation change. Decreased species are on the right, increased ones are on the left

Table 7. PCA

Axes	1	2	3	4	Total variance
Eigenvalues	0.362	0.159	0.073	0.068	1.000
Cumulative percentage variance of species data	36.2	52.1	59.4	66.2	
Sum of all eigenvalues					1.000

right (the terms "increased" and "decreased" species relate to their abundance). The basic characteristics of redundancy analysis (RDA) are summarized in Table 8. 31.1% of the vegetation variability along the main floristic gradient can be attributed to temporal change. A comparison of eigenvalues of the first ordination axes from PCA and RDA_{time} shows that about 90% of the vegetation variability along the main floristic gradient can be attributed to temporal change (Tables 7 and 8). Permutation test of the constrained axis is highly significant (Table 9).

The species which are most increased in 2006 indicate a nutrient-rich site (Bobbink et al. 1998). *Mycelis muralis*, *Rubus idaeus*, *Stellaria nemorum*, the species characteristic of nitrogen-rich sites, are reported to have increased in European nitrogen-polluted forests, following the drastic increase in atmospheric nitrogen inputs in Europe since the early 1980's (Bobbink et al. 1998). In comparison with 1934, in 2006 semi-decomposer species predominated in the plot, which could be caused by nitrogen pollution, but they can also indicate the stage of stand disintegration. Comparing old and new relevés, the most significantly decreased species are typical of the spring season (e.g. *Anemone nemorosa*, *Isopyrum thalictroides*), so different seasons of vegetation mapping could be one of the main reasons for such a decrease.

Significant changes were found in the species composition of herb layer. An increase in the homogeneity (composition of the herb layer is poorer and uniform) of phytocoenosis (Fig. 5) is the most apparent trend. Whereas in 1934 the species were distributed unequally and the phytocoenosis was richer, in 2006 the phytocoenosis is more uniform. In 2006 disappearance of rare species is obvious (e.g. *Doronicum austriacum*, *Gentiana asclepiadea*, *Pulmonaria filarszkyana*, *P. obscura*).

CONCLUSIONS

Repeated measures and observations in plot No. 12 proved that the studied forest represented

Table 8. RDA (environment factor is time)

Axes	1	2	3	4	Total variance
Eigenvalues	0.311	0.171	0.076	0.072	1.000
Species – environment correlations	0.937	0.000	0.000	0.000	
Cumulative percentage variance of species data	31.1	48.2	55.8	63.0	
Cumulative percentage variance of species – environment relation	100.0	0.0	0.0	0.0	
Sum of all eigenvalues					1.000
Sum of all canonical eigenvalues					0.311

Table 9. Monte Carlo permutation test (where a null hypothesis of the independence between the corresponding rows of the species data matrix and of the environmental data matrix was verified)

Summary of Monte Carlo test	
	Trace = 0.311
Test of significance of all canonical axes	*F*-ratio = 13.529
	P-value = 1.0000

an original natural ecosystem *sensu* KORPEĽ (1989) with timber volume typically evenly stratified between diameter classes, with characteristic mosaic of small spots of developmental stages and phases in the plot, and with distinct volume of lying deadwood. Changes that took place in the studied forest since the 1930's were not influenced by human activities, and hopefully, thanks to its position in the Carpathian Biosphere Reserve, this natural course of the forest development will be maintained in future. For better understanding of the developmental cycle of the studied forest and changes in the tree species composition within this cycle, more analyses of Zlatník's plots have to be carried out in future, desirably repeatedly at intervals of 10–15 years.

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Vývoj smíšeného horského pralesa během 70 let na trvalé ploše v Ukrajinských Karpatech

ABSTRAKT: V letech 2004–2006 byla na území Zakarpatské Ukrajiny v masivu hory Pop Ivan Maramurešský obnovena trvalá výzkumná plocha č. 12, založená ve třicátých letech 20. století. Synusie dřevin je tvořena dominantním bukem, přimíšenou jedlí a smrkem a skupinkovitě vtroušeným javorem klenem. Po 70 letech se zčásti změnilo procentuální zastoupení dřevin. Celková zásoba živých stromů se zvýšila z 527 na 636,4 m^3/ha. Zatímco u buku došlo k výraznému nárůstu hmoty, u jedle, smrku a klenu se zásoba téměř nezměnila. Celkový počet stromů (silnějších než 3 cm ve výčetní výšce) se zvýšil ze 737 na 760 ks/ha, u buku je však zvýšení počtu výrazné; pokles naopak zaznamenala jedle a smrk. Zajímavé výsledky přinesla obnova tzv. trvalého čtverce o velikosti 20 × 20 m, která prokázala, že buk je schopen s minimálními výškovými a tloušťkovými přírůsty setrvat v zástinu i přes 70 let.

Klíčová slova: trvalé plochy; prales; dynamika vývoje porostu; Ukrajina

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