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The succession dynamics in karst landscape after wind disturbances of *Picea abies* L.

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Abstract: Current views hold that ecological succession is not a simple process. Secondary succession is a consequence of numerous, diverse and complex interactions initiated by disturbances that create opportunities for establishment and renewal of complex life forms within ecosystem. Life history characteristics, interspecific interactions and recent environment combine to create repeatable changes in community composition over time heading towards a climax. The paper presents results of the ecological analyses of succession processess after wind disturbance of artificial spruce ecosystem, established instead of the original *Fagetum typicum* group of forest types. As an example of natural ecosystem is presented the *Fageto-Quercetum* group of forest types. Succession of the herb layer is firstly reflected in changes of species abundance and later in changes of dominant species and composition of plant communities. After the wind disturbance of spruce forest the succession started by emergence of heliophilous and eutrophilous beech herbal components, as well as nitrophilous species. Disturbance has speeded up the transformation of artificial spruce forests to natural mixed beech-oak forests that are ecologically much more stable.

Keywords: dynamics, ecological succession, wind disturbance, spruce monoculture, karst landscape.

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Introduction

Ecologists have distinquished between primary succession on sites without existing vegetation and secondary succession on sites with established vegetation. Secondary succession occurs after disturbances disrupt established communities, but without complete elimination of all life. Secondary ecological succession is nearly a universal phenomenon of characteristic sequential changes in species composition following either natural or anthropogenic disturbances. Windstorms, fires, clear cuts, mining, and agriculural clearings all provide the kinds of disturbances that set the stage for secondary succession (MORIN 1999).

When explaining succession plant ecologists traditionally focused on vegetation changes. However, succession leads also to corresponding changes in the composition of animal, fungi, bacteria, and protist communities (MORIN 1999). ODUM (1969) viewed succession as an orderly and predictable pattern of community development that produced significant changes in numerous and variable ecosystem attributes. In his view, succession culminates in a stabilized (climax) ecosystem in which biomass conservation and levels of symbioses are maximized per unit of energy flow into the system, despite the fact that productivity decreases in this phase.

Some ecologists suggest that the phrase „plant succession“ should be replaced by „comunity dynamics“ to emphasize that the population dynamics of interacting organisms are ultimately responsible for sequential successional patterns (MORIN 1999). Dynamics is a certain power, generally described as the changes of a system occurring at certain time intervals, which are largely resposible for its integrity. The term „community dynamics“ could describe the overall process of temporal change in community composition, thereby emphasizing that succession involves the dynamics of the entire complement of species interacting in communities, not just the vegetation.

To understand the theory of ecological succession also from a point of view of non-equilibrium thermodynamics we should start with view of some prominent ecologists that the main driving force behind the communities sequential changes is represented by energy flows both inside the ecosystem and from its surroundings (WÜRTZ & ANILLA 2010, JÖRGENSEN & SVIREZHEV 2004, ODUM 1969). And the ecosystem energetics is subordinated to the „maximum power principle“, which means that ecosystem always strives to develop such a structure and dynamics of the living systems (on all levels of hierarchy - from ecosystems to communities, from populations of species to organisms, from tissues to cells, etc.), which allows the most efficient use of available (free) energy as well as other natural resources, as are esp. water and nutrients. From this perspective, the driving force behind the succession is an imbalance between ecosystem´s energy inputs and its energy disbursements. The different successional stages are all fuelled by accumulation of the energy of biomass and nutrients (WÜRTZ & ANILLA 2010), which require new, more efficient dissipative structures and dissipative processes to cope with additional energy (KAY 2000, SABO 2011). New dissipative structures mean also the changes of species occurrence and abundances, leading to changes of communities composition, its stratification, complexity, etc.

In other words, consequent accumulation of biomass and nutrients in the successional stages means that a higher quality energy (exergy) is available in the ecosystem, which (in the sense of the 2nd Law of Thermodynamics) „is compelled" to react to this growth of the energy supply and to develop more complex dissipative structures and processes (JÖRGENSEN & SVIREZHEV 2004, SABO et al. 2010, 2011). This includes a spontaneous change of the biocoenoses composition in order to increase their capacity to accumulate more exergy (in the form of biomass and nutrients) and to dissipate the incoming solar exergy through more efficient pathways. This process is reflected in the consequent increase of the numbers and proportion of K-strategists and in the decline of R-strategists, as well as in the decline of S-strategists.

The K-strategists assert themselves in conditions of the lower stress and disturbance intensities, with sufficient supplies of nutrients and water, which means that the produced biomass is richer and is much less disturbed. The higher rate of the K-strategists means that the higher numbers of organisms are able to live in the respected populations and communities (in an ecological equilibrium), i.e. it means that the carrying capacity of the habitat and ecosystem is higher (CHAPMAN & REISS 1999). R-strategists are able to live and disperse in habitats with high frequency and /or higher intensity of disturbances, which cause partial or complete destruction of a biomass. They are characterized by the maximum rate of the population size growth. S-strategists tolerate stress well, thus live in the habitats with permanently poor conditions (esp. lack of nutrients, water, solar radiation). K-strategists dominate the natural forest communities, while K-R-S strategists prevail in the forests relatively close to nature (KRIŽOVÁ et al. 2010). Consequently, in natural forests are typical larger gilds on higher trophic levels, due to richer food supply (i.e higher quality energy) available on the lower levels (WÜRTZ & ANILLA 2010), simply to say, due to their higher carrying capacity than in case of spruce monocultures.

Non equilibrium theory (MORIN1999) predicts that equilibrium community cannot be realized because of interruption of succession toward equilibrium conditions by major disturbances. The non-equlibrium theory should be distinguished from the concept of non-equilibrium thermodynamics of living systems. According to the latter one outlined above, every input of energy causes a displacement of such a system from the point of thermodynamic equilibrium, the higher is energy input, the greater is this displacement (KAY 2000, SABO et al. 2011).

In this paper we analyze successional changes in species composition in the karst landscape in the context of forest life strategies.

Vegetation succession and global climate change

Our world has warmed quite a lot over the past 100 years (IPCC 2013). The linear trend of the increase of the average air temperature near the Earth´s surface (measured by a number of monitoring stations) indicates the 0.78 °C rise of the temperature between the periods 1850-1900 and 2003-2012, while the European continent has warmed even more, by 1.3 °C and these changes are higher towards the North Pole (EEA 2012). Each of the last three decades has been successively warmer at the Earth's surface than any preceding decade since 1850. In the northern hemisphere, 1983-2012, was likely the warmest 30 year period of the last 1,400 years and it is extremely likely that human influence has been the dominant cause of the observed warming since the mid 20th century (IPCC 2013).

This is clear from the positive radiative forcing, numerous measurements of the temperature rise as well as phenological and ecological observations and from deeper understanding of the Earth´s climate system and its drivers. The causes of the global warming (more precisely climate change) include esp. growth of the greenhouse gas concentrations in the atmosphere (esp. CO_2, CH_4, N_2O and others) and decrease of the Earth´s CO_2 absorbers, esp. forest cover, mainly due to liquidation of the tropical forests. For example, the emissions of the most important greenhouse gas, CO_2, have reached 35,7 Gt in the year 2013 (OLIVIER at al. 2015). The global deforestation of the tropical forests has reached its peak of 15 million ha per year (in average) in the decade 1990-2000, while in 2000-2010 it has drooped just to 13 mil ha per year (FAO 2011).

Continuing huge emissions of greenhouse gases, deforestation and degradation of forests will cause further warming and changes in all components of the climate system. Limiting climate change will require substantial reductions of greenhouse gas emissions, as well as forests protection (FAO, 2011, IPCC 2013).

One of the main aspects of global warming is a long term increase in temperature and changes in precipitation patterns, decrease of snow cover and ice. A whole range of climate change impacts is observed on ecosystems and on human society; while more and numerous further climate change impacts are expected in the future (EEA 2012). These include also an increase in the frequency and intensity of extreme climatic events such as extreme droughts and floods. The damage costs caused by natural disasters have already largely increased (EEA 2012).

Raising concern on extreme climatic events has triggered research on vegetation shifts (GALIANO et al. 2010, SMITH 2011, LLORET et al. 2012, MORIÁN-LÓPEZ et al. 2014, MERLIN et al. 2015). In the recent decades many studies have addressed the issue of the impact of global warming on vegetation succession and change of tree species composition of forest ecosystems (MERLIN et al. 2015, LLORET et al. 2012, MICHELOT et al. 2012). The most complete review of current theoretical and practical studies on the impact of global warming on the dynamics of changes of vegetation is provided by LAWSON et al. (2015). According to these authors species' responses to environmental changes such as global warming are likely to depend not only on what environmental conditions are like on average, but also on how much they fluctuate through time. Environmental variance can affect species' responses to global change via two different routes. At first, changes in environmental variance may have effects that are independent of the changes of mean environmental variables: for example, by exposing individuals to more extreme conditions, increased environmental variance may amplify population fluctuations, increase extinction risk, and select for bet-hedging adaptations that reduce temporal fluctuations in fitness. Second, the effects of environmental fluctuations may interact with changes in the „mean environment“. Organisms may respond differently to changes in mean environmental conditions depending on whether such changes occur gradually year-after-year, as typically assumed in global change studies, or erratically, as often occurs in reality.

Climate change is expected to modify the spatial distributions of zonal forest communities and thus, their species compositions (LANGE et al. 2012). The hypothesis of the impact of climate change on the structure of vegetation became of great importance in the planning and management of habitats management. But the differences of vegetation response to climate change and the unreliability of information sources require careful examination of issues before the results of studies are applied in the decision process. The previous studies suggest that the impact of climate change is reflected more in the lowlands. However, there exist a number of critical remarks, which disagree with models the impact of climate change on vegetation succession in mountain conditions (DHÔTE 1994, GALIANO et al. 2010, LLORET et al. 2011, SMITH 2011, MICHELOT et al. 2012, VILÁ-CABRERA et al. 2013, MORÁN-LÓPEZ et al. 2014, HAWKES & KEITT 2015, LAWSON et al. 2015).

Climatic extremes may affect the forest ecosystems as disturbance factors. In the context of extreme natural events such as windstorms, floods, long-term droughts, forest fires, pests outbreaks, etc., many authors point to the fact that natural forest ecosystems with their specific structure and specific microclimate react better to stressful effects of global warming, which is expressed by their resistance, recovery and resilience characteristics (HAWKES & KEITT 2015).

Ecological resistance is the capacity of an ecosystem, species or individual to remain basically unchanged when it is subjected to a disturbance. Resilience is the ability to recover pre-disturbance structures and functions after a disturbance has passed. However, resilience has its limits concerning both the scope and intensity of disturbances. Therefore, at the ecosystem level, the tree composition, structure and distribution of forests as well as the water, carbon and nutrient cycle are expected to be modified in the context of climate change (BRÉDA et al. 2006, GALIANO et al. 2010, CHEAIB et al. 2012, CAVIN et al. 2013).

The aim of the present paper is to evaluate changes in the forest habitats at stationary areas with wind disturbance of monocultural *Picea abies* forest of the Slovak Karst which occurred as a result of natural succession of woody vegetation over the last 25 years.

Study area

Slovak Karst National Park (hereafter NP) is situated in the South-East Slovakia. Significant part of the area can be characterized as the semi-mountain relief, to a certain degree divided into the system of valleys, furrows and basins, which is surrounded by intermountain basins from the South and East. Its 43-km long southern boundary coincides with the Slovak border with Hungary. The area is a series of plateaux whose maximum altitude ranges between 400 and 900 m. The summits of the Plešivec Plateau reach 851 m. The lowest point of 190 m a.s.l. is the Turna Valley, an area in the transition zone on the southern margin of the NP (SNC 2011).

The basic **geological** structural unit of the region is represented by the limestone complexes (Wetterstein limestones, Gutenstein limestones - pink and light blue-grey limestones and dark blue-grey dolomites, Steinalm limestones developed through the accumulation of the remains of various organisms).

The Slovak Karst is a distinct geomorphological unit, classified as a karst with elevated upland plateaux surrounded by steep slopes descending to adjacent basins, valleys, and gorges. Karst phenomena are created by the corrosive and erosive activities of water in soluble limestones. These are both primary (lapiés, karst depressions and valleys, sinkholes, karst springs, chasms, caves) classified as surface or underground, and secondary (dripstones, travertines). There are also many vertical cave systems, or chasms (VOLOŠČUK et al., 2016).

The variety of **soil types** reflects the region´s heterogeneous geological composition. Rendzina type soils occur on carbonate bedrocks, with cambisols in adjacent basins; cambisols and luvisols occur on non-carbonate bedrocks, and hydromorphic soils on the bottom of valleys. Limestones, dolomites, and their scree at the base of slopes are covered by the products of long-term weathering and fossil soils (terrae calcis). In addition, plateau surfaces broken by lapiés and sinkholes are covered by rendzinas, luvisols, and protorendzinas. Cambisols and rendzinas are characteristic of plateau sites with fewer fine karst forms and with thicker weathering deposits, often continuously covered by oak-hornbeam forest (SNC 2011, IUSS 2014).

The area of Slovak Karst was officially declared as the Protected Landscape Area (PLA) in 1973 (ROZLOŽNÍK & KARASOVÁ 1994). The territory of PLA was declared a National Park, on March 1, 2002 and classified in Category II of the IUCN Protected Area Category System. The protected territory has an area of 361.7 km^2 and is surrounded by a prevention zone of 383.3 km^2. Geographical coordinates (latitude and longitude): N 48°28' - 48°43'; E 20°15' - 21°01'.

In 1977, the Bureau of the UNESCO International Coordinating Council of the Man and the Biosphere Programme designated the PLA and its prevention zone within the UNESCO´s international system of Biosphere Reserves (BR).

The caves situated in Slovak karst National Park and the adjacent Aggtelek National Park in Hungary on December 9, 1995 have been included to the UNESCO World Heritage List.

The research of Slovak Karst Nature has a long history (VOLOŠČUK 1993). In 1981 – 1990 the complex interdisciplinary research was provided by the Slovak Institute of Monument Protection and Nature Conservation in Bratislava. An important forestry research has also been undertaken. The expert team of this research established permanent (stationary) research plots in 1983-1985 to study the structure and dynamics of the natural forests and non-forest ecosystems. In the year 2010-2012 the stationary permanent plots were restored and biometrical measurements were realized using the same methods as in 1985. The research in non-forest ecosystems of stationary areas was focused on the vegetation succession. Forests are a significant landscape element, which create the characteristic feature of the landscape and contribute to its ecological stability (VOLOŠČUK et al. 2011).

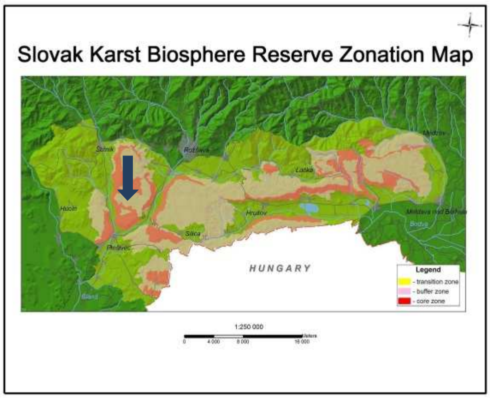

Fig.1. Location of Plešivská Plateau in Slovak Karst territory ⬇

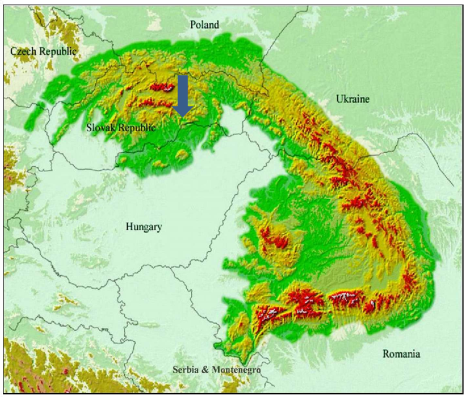

Fig.2. Location of Slovak Karst Mts in Carpathians ⬇

Methods

Repeated phytosociological records of vegetation were made in stationary area S7 and S11 at area of 10 x 20 m in 1985 (7a, 11a) and on the same areas in 2010 (7b, 11b). The coverage of each of levels (E3, E2, E1, E0) the registration area, was estimated in percentage cover of individual species of vascular plants in Braun-Blanquet scale (BRAUN-BLANQUET 1964) extended by VAN DER MAAREL (2007). Entries have been saved in the database program TURBOVEG (HENNEKENS & SCHAMINÉE 2001). Nomenclature of the plant species is united by MARHOLD & HINDÁK (1998). Nomenclature of the forest types is according to ZLATNÍK (1959). To evaluate the phytosociological entries we used the programs JUICE (TICHÝ 2002, TICHÝ & HOLT 2006, TICHÝ & CHYTRÝ 2006) and CANOCO (TER BRAAK & ŠMILAUER 2002). To evaluate changes in fundamental ecological factors by phytoindication we used indirect information provided by Ellenberg indicator values (ELLENBERG et al. 1992). They were evaluated not only from the aspect of species composition, but also concerning their relations to the key environmental gradients (light, temperature, continentality, soil reaction, nitrogen content). For the evaluation of species diversity, we used the Shannon index, Jaccard index and Sörensen index (SHANNON & WEAVER 1963). The map output was processed in ArcMap 9.2.

Results

Phytocoenological characteristics of stationary areas

S 7 – Plešivská Plateau, N 48°35.224,E 20°24.602, Group of forest types: *Fageto-Quercetum* Zl. 59. 520 m a.s.l., SE, slope 10°, E3 (1985/2010) *Quercus petraea* 38/64%, *Carpinus betulus* 45/16%, *Fraxinus excelsior* 11/13%, Acer sp. 5/6, *Fagus sylvatica* 1/1%, E2 *Carpinus betulus* 20/20%

E1 1985: *Carex pilosa* 4, *Galium odoratum* 2b, *Dentaria bulbifera* 2m, *Fragaria vesca* 2m, *Galeobdolon luteum* 2m, *Waldsteinia geoides* 2m, *Asarum auropaeum* 2m, *Anemone nemorosa* 1,*Tithymalus amygdaloides* 1, *Glechoma hirsuta* 1, *Melica uniflora* 1, *Mercurialis perennis* 1, *Pulmonaria angustifolia* 1, *Stellaria holostea* 1, *Aegopodium podagraria* 1, *Acer campestre +, Ajuga reptans +, Asarum europaeum +, Bromus benekenii +, Campanula rapunculoides +, Campanula trachelium +, Carex michelii +, Cornus mas +, Crataegus laevigata, +, Corydalis cava +, Cruciata glabra +, Dactylis polygama +, Daphne mezereum +, Fraxinus excelsior* +, *Galium aparine* +, *Galeopsis pubescens +, Geum urbanum +, Heracleum sphondylium +, Hordelymus europaeus +, Hypericum hirsutum +, Isopyrumthalictroides +, Lathyrus vernus +, Ligustrum vulgare +, Neottia nidus-avis +, Polygonatum multiflorum, Quercus dalechampii +, Sorbus torminalis +.*

E1 2010: *Carex pilosa* 4, *Dentaria bulbifera* 2b, *Galium odoratum* 2b, *Waldsteinia geoides* 2m, *Asarum europeaum* 2m, *Anemone nemorosa* 1, *Fragaria vesca* 2m, *Galeobdolon luteum* 2m, *Glechoma hirsuta* 1, *Melica uniflora* 1, *Mercurialis perennis* 2m, *Pulmonaria angustifolia* +, *Stellaria holostea* 1, *Aegopodium podagraria, Acer campestre +, Ajuga reptans +, Bromus benekenii +, Campanula trachelium +, Carex michelii, Cornus mas +, Crataegus laevigata +, Corydalis cava +, Cruciata glabra +, Dactylis polygama +, Daphne mezereum +, Fraxinus excelsior +, Galium aparine +, Galeopsisi pubescens +, Geum urbanum +, Heracleum sphondylium +, Hordelymus europaeus +, Hypericum hirsutum +, Isopyrum thalictroides +, Lathyrus vernus +, Ligustrum vulgare +, Neottia nidus-avis +, Polygonatum multiflorum +, Pulmonaria angustifolia +, Quercus dalechampii +, Sorbus torminalis +.*

S 11 – Plešivská Plateau, N 48°37.503, E 20°24.263, Group of forest types: *Fagetum typicum* Zl. 59. 620 m a.s.l., NW, slope 5°, E3 *Picea abies* (1985/2010) 90/0-wind disturbance, *Quercus petraea* +/0, *Populus tremula* +/0. E2 *Carpinus betulus* +/0, *Fagus sylvatica* +/0, *Corylus avellana* +/0. Tree succession <30 cm *Carpinus betulus* 20%, *Fagus sylvatica* 10%, *Picea abies* 10%, *Acer pseudoplatanus* 5%.

E1 1985: *Galium odoratum* 3, *Dentaria bulbifera* 2m, *Moehringia trinervia* 2m, *Viola reichenbachiana* 2m, *Mercurialis perennis* 1, *Pulmonaria obscura* 1, *Aconitum mioldavicum* +, *Alliaria petiolata +, Brachypodium sylvaticum +, Cardamine impatiens +, Daphne mezereum +, Dryopteris filix mas +, Festuca altissima +, Galium aparine +, Galeopsis pubescens +, Geranium robertianum +, Horedlymus europaeus +, Hypericum perforatum +, Melica uniflora +, Mycelis muralis* 1, *Neottia nidus-avis +, Poa nemoralis +, Symphytum tuberosum +, Urtica dioica +.*

E1 2010: *Galium odoratum* 5, *Brachypodium sylvaticum* 4, *Mercurialis perennis* 4, *Urtica dioica* 4, *Dentaria bulbifera* 2b, *Dryopteris filix mas* 2b, *Moehringia trinervia* 2b, *Galeobdolon luteum* 2m, *Glechoma hederacea* 2m, *Rubus hirtus* 2m, *Symphytum tuberosum* 2m, *Maianthemum bifolium* 1, *Pulmonaria obscura* 1, *Tithymalus amygdaloides* 1, *Tithymalus cyparissias* 1, *Lilium martagon* +..

Tab. 1. Indicator values according to Ellenberg (1992) and difference between two monitored years (1985, 2010) of stationary relevé 11 an 7 in Slovak Karst National Park (ex Vološčuk et al. 2016)

Relevé	Year	Ellenberg Indicator Values						
		Light	Teperature	Continentality	Moisture	Soil Reaction	Nutriens	No. of All Species
11	11a – 1985	4.9	5.2	3.7	5.3	6.4	5.8	60
	11b - 2010	4.1	5.2	3.7	5.1	6.0	5.8	20
	Difference	-0.8	0.0	0.0	-0.2	-0.4	0.0	-40
7	7a – 1985	4.8	5.3	3.7	5.0	6.9	6.0	50
	7b - 2010	3.5	5.3	2.8	5.2	6.7	7.0	7
	Difference	-1.3	0.0	-0.9	0.2	-0.2	1.0	-43

Tab. 2. Indices of species diversity of stationary area in Slovak Karst National Park

Relevé	7a	7b	11a	11b
Richnes	60	20	50	7
S-W index	3.26	1.90	2.76	1.55
Evenness	0.78	0.62	0.70	0.71

Discussion

Stationary area S 7

Between 1985 and 2010 in the beech-oak forest ecosystem *Fageto-Quercetum* Zl. 59. came about significant changes in tree composition and number of tree species. Significantly increased participation of competitively strong K strategist *Quercus petraea* at the expense of K-R strategist *Carpinus betulus. Fraxinus excelsior* is K-R-S strategist with the ability to endure stress and quickly occupy the forest gaps after disturbances. The total crown canopy fell in that period from 95% to 85%. This is reflected in the change in total volume of timber, circular base and the number of trees. In layer E2 share of *Carpinus betulus* in both periods was 20%, indicating its ability to assert themselves compared to their oak competitors with longer period of vegetative growth in youth. Natural regeneration of oak and beech particularly in the layer to 50 cm is favourable. The best naturally restoring K-R-S strategist is *Fraxinus excelsior*. Natural regeneration of oak, beech and ash are undermined by herbivorous animals. This causes disruption of the forest ecosystem natural reproductive cycle (Vološčuk et al., 2016).

The analysis of the ecological numbers points to the fact that within the period 1985 – 2010, apart from the nutrient number, no significant changes were recorded, esp. concerning light, temperature, moisture and soil reaction. Concerning the contents of nitrogen in the soil a small shift was recorded from the index of the species of the moderately rich soils to the index of species of moderately rich and rich soils.

The statistical analysis of the content of nitrogen shows a positive correlation. In comparison with the year 1985 the correlation between soil reaction and nitrogen content has been lost, as well as between temperature and nitrogen. This can be explained by the seasonal dynamics of the abundances of plant species requiring more humus and nitrogen in the soil and also by the „tree dynamics“ – change of the woody species representation in the past 25 years.

Similarity index (Jaccard index 100%, Sörensen index 100%) of plant communities of the two periods shows a relative stability of the structure of the *Fageto-Quercetum* plant community (Cn 76.10% and 75.85%).

Stationary area S 11

This area is interesting in that the original habitat typical beech forests *Fagetum typicum* Zl. 59 was in the early 20th century planted with spruce *(Picea abies)* monocultures. In 2004 this spruce forest was affected by windbreaks. Altitude 620 m a.s.l. The slope of 3-5 degrees. Soil is rubefic rendzinas.

Tree species composition in 1985: spruce 100% in dominant stand. Beech *Fagus sylvatica*, hornbeam *Carpinus betulus*, oak *Quercus petraea* and aspen (*Populus tremula*) are present in secondary layer. In the layer to 50 cm in the low values of coverage are occurring sycamore maple, Norway maple, hornbeam and beech. The coverage of herbs layer was 60-90%. Dominant and subdominant herbs occurring in the beech forests are *Galium odoratum* and *Dentaria bulbifera*. Spruce forests ecosystems in Plešivská Plateau occur generally in inverse areas of karst sinkholes or depressions with flat earthed surface. The tree species composition is dominated by *Picea abies*, whose authenticity in Plešivská Plateau is not yet clearly scientifically interpreted. During the spread of vegetation in the postglacial time (atlantic period -5,000 years), the spruce in the Slovak Karst was a native species (LOŽEK 1973).

Frequency distribution of tree diameters (at the height of 1.3 m) on a stationary area in 1985 with domination of *Picea abies* was symmetrical in the range of 14-60 cm. The prevailing number of trees in diameter should be 32-36 cm. The average age of spruce was 90 - 100 years. The high-rice spruce curve was consistent with the curve of the uniform and even-aged spruce forests (VOLOŠČUK 1988 a,b, VOLOŠČUK et al. 2011).

Spruce forest ecosystem of stationary area in the period 1985-2004 was constantly disrupted by the windstorms and also by intentional harvesting of spruce. Due to the reduction of the canopy crowns litter mineralization has speeded up and the onset of nitrophilous vegetation was visible. Opening the side wall of spruce forests and consequent further windstorms have caused uprooting of many spruce trees, which allowed penetration of more nitrophilous vegetation elements into the area (VOLOŠČUK et al. 2016).

After removal of spruce stands on a stationary surface secondary succession has started. After the wind calamity in 2004 and removal of spruce, in the resulting area without trees started secondary succession with plant species requiring neutral soil, tolerant to light and rich in nitrogen (*Urtica dioica, Rubus hirtus, Brachypodium pinnatum).* After removal of spruce in natural regeneration dominated K-R-S life strategists maples *Acer pseudoplatanus* and *Acer platanoides* (67,000 units per ha), also ash *Fraxinus excelsior.* In a layer over 50 cm in addition to maple –a competitive K strategist *Fagus sylvatica* was maintained. Reducing the high number of individuals in the layer of 50 cm was caused mostly by herbivorous animals.

Changes in herbal layer of *Fagetum typicum* group of forest types after wind disturbance of artificial spruce monoculture reflect significant changes of conditions (onset of nitrophilous vegetation). Stationary surface is suitable for further long-term successional processes on the forests after the wind calamity. Comparison of Ellenberg indexes for plant communities from 1985 and 2010 shows a significant change in light and a slight increase of soil acidity (in 1985 index 6.4 in 2010 index 6.0) which is reflected in the occurrence of species of slightly acidic to neutral soils (cambisols). In the long term succession on this stationary area the community succession towards the beech oak forest admixed with maple, ash and linden can be clearly predicted.

The current state of ecological processes in forest ecosystems stationary surfaces allows to predict the direction of the development of ecologically stable natural forests in next 50-70 years, only in the event that the ecosystems will be protected from human disturbance.

Conclusion

The spruce forests on Plešivská Plateau in Slovak Karst National Park today are very labile ecosystems. In karstic sinkholes they have been artificially planted in the early 20th century. The main causes of their disturbance are wind storms. Due to synergy of windstorms and rise of the mean temeperatures the spruce forests in Plešivská Plateau conditions are unable to recover naturally. Disturbance speed up the transformation of artificial spruce forests for natural mixed beech and oak forests that are ecologically much more stable. As an example of the natural ecosystem is given stationary area 7 with the community of *Fageto-Quercetum Zl. 59.*

The state forestry and state nature conservancy administrations face especially these two options:

- lead the development of natural ecosystems in stationary areas for environmentally stable climax communities irreplaceable for scientific research and with cultural ecosystem services (educational-environmental functions), or
- ensure their rational economic use for the purpose of gaining maximum benefit from forest ecosystem services.

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