Vegetation succession over broad geographical scales: which factors determine the patterns?

Sukcese vegetace v širším geografickém měřítku: jaké jsou určující faktory?

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We reviewed 37 studies on vegetation succession in which the succession started on bare ground, was followed in at least six sites, and where these sites were spatially separated over at least 10 km^2. The effect of environmental factors, which were explored in at least five studies, on the course of succession was assessed, based on the proportion of significant and non-significant results. Surrounding vegetation, macroclimate, soil moisture, amount of nitrogen and soil texture appeared to have the highest influence on the course of succession. Less influential were the size of a disturbed site, pH, organic matter and phosphorus content. Surrounding vegetation exhibited a significant effect in all cases where this was considered. These results imply that succession cannot be studied without the landscape context. The large-scale approach to succession has the potential to contribute substantially to both the theory of succession and practical applications, especially in restoration ecology.

Keywords: environmental factors, landscape context, restoration ecology, species pool, vegetation succession

Introduction

An enormous number of published studies on succession deal with one or several, more or less comparable sites (e.g. Burrows 1990, Glenn-Lewin et al. 1992, Walker & del Moral 2003). In these studies, succession is often described in remarkable detail, often using experimental manipulation of environmental factors or vegetation itself, thus testing various hypotheses on mechanisms of vegetation change (Tilman 1988, van der Maarel 2005). However, there are not many studies that evaluate succession over broad, i.e. landscape, regional or even continental, scales (van Andel et al. 1993, Walker & del Moral 2003). Those attempts that have been made at this scale are often based on intuitive, not quantitative, comparisons of a high number of seral stages. It is obvious that quantitative studies on succession on a broad geographical scale cannot easily test hypotheses on mechanisms, but they do provide a good opportunity to test hypotheses on pattern. For various reasons, this opportunity has not been appropriately exploited so far. Studying vegetation dynamics over broader geographical scales can provide a useful framework to detailed studies, supporting well-balanced interpretations of results. Using the broader approach, we can generate hypotheses which can be subsequently tested at small scales. Obviously, small-scale experimental studies and large-scale studies can be seen as complementary approaches.

Among the first attempts to describe successional changes in vegetation over larger scales were the studies of early generations of European phytosociologists. By the traditional descriptive approach (using phytosociological relevés) they often analysed many particular sites and then tried to depict intuitively general successional trajectories using formally described plant communities (associations) or dominant species (Ellenberg 1988). These studies provided a useful, though limited overview over vegetation dynamics especially in the case of rapidly changing vegetation such as that on various ruderal sites in urban or industrial habitats (Pyšek & Pyšek 1988). Resulting general schemes were often helpful for urban or landscape planning (Laurie 1979).

Advances in computer technology and multivariate techniques enabled researchers to elaborate a large number of vegetation records (Jongman et al. 1987), including those from seral stages. Thus, it seems that the number of studies dealing with succession on broad scales has been increasing. Here we review these studies and address the question: Which environmental variables determine the course of succession over broad geographical scales?

Which seres have been studied?

We have found 37 studies which match the following arbitrarily selected criteria: they deal with at least 6 sites, usually representing different particular seral stages, which were spread over at least 10 km^2 (Table 1). We considered only seres which started on bare ground in which the succession was followed from the very start. Old fields and various mining sites were most frequently investigated (Walker & del Moral 2003). Environmental factors considered in the particular studies are listed in Table 1. Those factors, whose influence on the course of succession (defined here as changes in vascular plant species composition) was statistically tested in particular studies, are indicated in Table 1.

We are aware of the limitations of the data set extracted from the heterogeneous studies which can be hardly mutually compared in a detail. Thus, we concentrate only on the most robust patterns. Causal influences of the environmental factors on the course of succession are differently dealt with in the studies, not enabling us to make clear and undoubted generalizations. Therefore only selected aspects are tentatively discussed further.

The studies differed in the number of the sampling plots and in the area covered. It must be mentioned that the same number of sampling plots spread over the same area need not be equally representative in different situations. For example, within a homogenous landscape a small local study can be representative for the whole area, but not so in a heterogeneous landscape. Most studies on succession are scaled a priori by human-caused or natural disturbances and sampling follows the pattern. This introduced another component of heterogeneity into the data set. Whether a factor exhibited a statistically significant influence on the course of succession (Table 2) depended largely on the range of values dealt with in the particular studies. Generally, there is obviously higher probability of significant influence if the range is broad (Jongman et al. 1987). The studies differed considerably in this regard, thus further weakening the strength of our conclusions. Despite this limitation, the importance of the particular environmental factors is clearly seen from Tables 1 and 2.

Table 1. – Studies on vegetation succession at broad geographical scales and environmental factors considered. In those studies which used rigorous statistics, the factors which appeared to be significantly correlated with successional pattern are given in bold. For those studies which did not use statistics, only factors which were reported to obviously influence the course of succession are listed (in italics).

Type of succession	Geographical area	Factors	References
1. Mining sites			
Gravel-sand pits	Czech Republic (36 pits; 78,000 km^2)	**age**, **proportion of arable land**, **urban land**, dry grasslands, pastures, **wet grasslands and woodland up to the distance of 1 km from a pit; presence of dry grassland**, **wet grasslands,** pastures, forest fringes **and woods up to 100 m from sampling site**; **altitude**; **mean annual precipitation**; **mean annual temperature**; **pH**; **water table proportion of gravel,** sand, clay and **silt**	Řehounková & Prach (2006)
Gravel pits	Sweden (68 pits; 700,000 km^2)	*age, surrounding vegetation type up to 100 m wide zone around the pit, area, macroclimate, pH,* total N, *C/N, P, K, texture*	Borgegård (1990)
Basalt quarries	Czech Republic (56 quarries; 1800 km^2)	**age, presence of dry grasslands in the surroundings, mean annual precipitation, mean annual temperature**	Novák & Prach (2003), Novák & Konvička (2006)
Limestone quarries	Canada: S Ontario (18 quarries; 70,000 km^2)	**age, density of trees adjacent to the quarry, latitude, inclination, quarry size, substrate instability, habitat type (wall, floor, top)**	Ursic et al. (1997)
Open-cast mining	Germany: Lower Lusatia (50 sites; 5000 km^2)	*age, dispersal, locality, pH, conductivity, maximum water capacity, amount of nitrate-nitrogen, total N, phosphate, organic C, P, sulphate, total sulphur*	Wiegleb & Felinks (2001a, b), Schulz & Wiegleb (2000)
Colliery waste heaps	England: S Lancashire (86 sites; 56 km^2)	*age, pH, texture, hill/hollow topography*	Molyneux (1963)
Coal strip mines	USA: Oklahoma (49 coal strip mines; 21,000 km^2)	**age**, **soil moisture**, pH, **total N,** total P, **K, Ca, Fe, Mn, Cu**, Zn, texture (gravel, sand**, silt,** clay)	Johnson et al. (1982)
Surface coal mine	USA: North Dakota (6 sites; 26 km^2)	*age, aspect, slope, pH, water saturation, conductivity, total N, P, Ca, Mg, K, Mn, Na,* SO_4*, clay, silt, sand, bulk density*	Wali (1999)
Harvested peatland	Finland: central part (8 sites; 25,000 km^2)	**age, surrounding vegetation, conductivity, ash content, ammonium nitrogen content, nitrate nitrogen content, soluble P, mean particle size of surface peat, thickness of peat layer**	Salonen (1994)
2. Old fields and plantations			
Old fields	Canary Islands: Tenerife (11 fields; 100 km^2)	**age, surrounding vegetation, mean annual precipitation, moisture**	Otto et al. (2006)
Old fields	USA: New York (21 sites; 600 km^2)	*age, dispersal, previous land use, moisture*	Stover & Marks (1998)
Old fields	The Netherlands: E part (80 sites; 10,000 km^2)	**age, soil types**	Smit & Olff (1998)
Old fields after topsoil removal	The Netherlands (9 fields; 30,000 km^2)	*age, surrounding vegetation, field area, organic matter*	Verhagen et al. (2001)

Type of succession	Geographical area	Factors	References
Old fields	Romania: Transylvanian Lowland (40 old fields; 12 km^2)	**age, relative area of propagule sources (grasslands)**, **propagule availability (grasslands)**, dispersal mode, field area, slope, exposure	Ruprecht (2005, 2006)
Old fields	Czech Republic (108 sites; 250 km^2)	*age, distance to propagule sources, moisture*	Osbornová et al. (1990)
Old fields	Finland (130 sites; 300,000 km^2)	*age, character of the surrounding landscape, previous cultivation of the field, latitude, site moisture*	Prach (1985)
Old fields	Spain: SE part (96 plots; 16 km^2)	**age**, **dispersal**	Bonet & Pausas (2004)
Old fields	Denmark (20 sites; 300 km^2)	**age, temperature, pH, moisture, nitrogen, light**	Ejrnæs et al. (2003)
Old fields	USA: Mississippi (40 sites; 1000 km^2)	**age, pH, organic matter, humus type, total C, total N, P, K, Ca, Mg, bulk density**	Switzer et al. (1979)
Abandoned ploughed pastures	Brazil: E Amazonia (15 sites; 2500 km^2)	**age, pasture-use history**, pH, organic matter, N, P, Ca, Mg, K, soil bulk density	Buschbacher et al. (1988)
Abandoned farmlands	Sweden – island in west coast (26 sites, 10 km^2)	**age, seed sources, dispersal mechanism, land use**	Olsson (1987)
Abandoned culture lands	Spain: S part (137 sites; 100 km^2)	**type of human disturbance (agriculture/fire), inclination, altitude, slope, pH,** conductivity, water field capacity, organic matter content, **clay, sand,** silt	Gallego Fernández et al. (2004)
Abandoned coffee plantations and pastures	Puerto Rico (28 sites; 150 km^2)	**age**, **land use, altitude**, degree of slope, slope aspect, percentage of soil clay	Marcano-Vega et al. (2002)
3. Others			
Islands	Sweden: lake Hjålmaren (30 islands; 670 km^2)	**age, dispersal, distance to mainland or to a large island, number of islands within 200 m distance from the studied island,** habitat diversity on an island, **perimeter of the island**, island shape	Rydin & Borgegård (1988)
Islands	USA: Louisiana, Atchafalaya Delta (6 sites-transects, 110 plots; 20 km^2)	**age**, **hydrologic regime (degree of inundation),** *grazing*	Shaffer et al. (1992)
Artificial islands	Czech Republic: Třeboň Basin (71 islands; 300 km^2)	**age, isolation, area, elevation**	Rejmánek & Rejmánková (2002)
Sand dunes	USA: Kreton (48 plots; 240 km along Oregon coast)	**age,** macroclimate, **microclimate**, **stabilization**	Kumler (1969)
Sand dunes	USA: Michigan (72 dune ridges; 20 km^2)	**age, wind velocity, evapotranspiration, sand movement, soil moisture,** pH, **total N, P, C, Ca,** Mg, K, **light availability**, sand burial, erosion, soil drying	Lichter (1998)
Wet dune slacks	Belgian and NW French coast (83 dune slacks; 1000 km^2)	**age, dispersal, isolation, area, moisture, pH, nitrogen, light**	Bossuyt et al. (2003)
Gravel bars	India: NW Himalayas (23 sites; 20,000 km^2)	*age, regional climax vegetation, elevation above the river, stand height, macroclimate*	Prach (1994)

Glaciers	USA: Alaska, Glacier Bay (10 sites; 1000 km^2)	**age**, **distance to seed source**, soil texture	Fastie (1995)
Landslides	Puerto Rico (46 sites; 44 km^2)	**age, particle size distribution, slopes,** pH, **organic N, C,** total P, available P, Mg, Ca, K	Guariguata (1990)
Clearcuts and burned forests	Canada (386 sites; 300,000 km^2)	**age, type of disturbance**, **soil moisture, soil parent material, soil texture**	Schroeder & Perera (2002)
Ombrotrophic mires	Canada: Québec (16 sites; 60 km^2)	*age, climate, human drainage, fire*	Pellerin & Lavoie (2003)
Sedimentation basins	Czech Republic (18 sedimentation basins; 20,000 km^2)	age, **plant species in surroundings up to 100 m distance,** pH, altitude, **origin of the deposits (ore-washery/ash-slag)**, length of perimeter of homogeneous sedimentary plots, content of chlo rides/sulphates	Vaňková & Kovář (2004)
Volcano	USA: Washington, St.Helens (103 plots; 254 km^2)	*age, dispersal ability, proximity of propagule sources, seed rain, isolation, substrate moisture*, *microtopography*, *nutrient condi tions, herbivory, deposit thickness, subsequent physical conditions*	Dale et al. (2005)
Post-fire sites	Canada: Québec (31,033 sites; 10,000 km^2)	*age*, *area*, *moisture*, *soil types, secondary disturbance*	Harper et al. (2002)

Table 2. – Frequency of significant and non-significant influence of the environmental factors on the course of succession as reported in the references listed in Table 1, and the total number of studies out of 37 listed in Table 1, in which the factor was considered regardless of whether its significance was tested. Results of both univariate and multivariate statistics were considered. Only those factors, which were evaluated at least in 5 studies, are included. The factor was considered as significant if at least one its parameter was significant (e.g. edaphic factors – together were considered as significant if at least one of a group of analysed factors was significant).

Factor	Number of studies	Significant	Non-significant
Age	36	23	1
Surrounding vegetation (incl. seed sources, dispersal, land use)	20	13	0
Size of a site	9	4	2
Macroclimate (incl. altitude)	12	7	2
Edaphic factors (together)	30	14	4
pH	14	5	5
Moisture	17	8	1
Organic matter	9	4	2
Nitrogen (various forms)	12	7	1
Phosphorus (various forms)	9	3	3
Soil structure (incl. soil types)	19	11	3

Important environmental factors

The frequencies in which the factors were reported as having significant or non-significant influence on the course of succession are listed in Table 2, together with the total numbers of studies in which the factors were considered, regardless of whether or not statistics were employed (see Table 1). Time, i.e. successional age, was naturally the most frequent variable to which the course of succession was related, and this factor nearly always exhibited a significant influence on the vegetation pattern. In some studies, the temporal patterns were suppressed by the influence of some abiotic factors if these had a large amplitude (Vaňková & Kovář 2004, Prach et al. 2007). However, the successional age is a major but not the only aspect of the temporal dimension. For example, the effect of starting date can also be important. Surrounding vegetation, expressed either as the occurrence of particular vegetation types, land use categories, occurrence of particular species, or dispersal categories around a considered site, had significant influence in all studies where it was considered. Nearly the same is true for macroclimate (temperature, precipitation, altitude and latitude), and for site moisture and nitrogen content among the edaphic factors. Soil structure was also highly influential, especially the content of soil particles such as clay or sand. Organic content, pH and phosphorus had significant influence only in some cases. At least some edaphic factors played a statistically significant role in nearly 80% of studies in which these factors were tested.

Macroclimate and surrounding vegetation can be considered as landscape factors. Edaphic factors, represented mostly by substratum quality, and the size of a site represent local site factors. The proportional influence of both groups of factors on the course of succession was only rarely evaluated in a quantitative way. In our study on succession in disused gravel-sand pits, the landscape factors together were responsible for vegetation variability in about 44%, and the local site factors in 23% in a CCA analysis. Time contributed about 10% and the rest was unexplained variability. Soil moisture was the most important of the edaphic factors (Řehounková & Prach 2006).

Surrounding vegetation and the role of the area of site

The fact that surrounding vegetation had a significant effect in all cases when it was tested implies that succession is a highly stochastic process if we consider only a particular site without considering the landscape context. Influence of the surrounding vegetation on succession is clearly manifested in species pool, which is determined by macroclimate, vegetation history, and land-use history (Zobel et al. 1998, Settele et al. 1996). Various studies demonstrated the decisive role of sources of diaspores in the vicinity of a disturbed site and intensity of transport of the diaspores (Fastie 1995, Ursic et al. 1997, Verhagen et al. 2001, Vaňková & Kovář 2004, Dale et al. 2005, Řehounková & Prach 2006). Because sites where succession proceeds can be seen as habitat islands, the theory of island biogeography can be applied to some extent (Bossuyt et al. 2003). The smaller the area of a site the easier, usually, is its colonization from close surroundings, and succession usually occurs faster and often directly towards restoration of a previous vegetation than in large sites (Dovčiak et al. 2005). In large disturbed sites, more ruderals have a chance to establish and eventually may arrest or divert succession. In some cases, succession on real islands, either natural or human-made, was studied (Rydin & Borgegård 1988, Rejmánek & Rejmánková 2002). In all those cases, area and isolation were the most important factors, determining especially the number of present species.

It seems that the propagule sources in close vicinity are usually decisive for the establishment of late successional, often target and mostly rather specialized groups of species with lower dispersal ability (Poulin et al. 1999, Novák & Prach 2003). Generalists, which are often present among early successional species, often belong to easily dispersed species, which can colonize a site from a longer distance (Grime 2002). Late successional, dry grassland species colonized basalt quarries with a high probability if they occurred up to the distance of 50 m (Novák & Konvička 2006). Detailed studies of the unique post-eruption landscape of Mt St. Helens revealed the important role of refugia and the distance to the untouched vegetation for re-colonization, but only up to about 100 m (del Moral et al. 2005). However, in the study conducted in chalk quarries in N England by Jefferson (1984) transport of diaspores of some target species was recorded up to the distance of several kilometres.

Macroclimate

The assumption that climate influences succession is trivial (Box 1981). It is, however, difficult to test because of the lack of directly comparable data and conclusions remain largely speculative (Walker & del Moral 2003: 262–266). Increasing precipitation increased stand height and biomass but also participation of alien species in an old-field succession in Tenerife island (Otto et al. 2006). In dry seres, species diversity increased permanently during succession, while it peaked early and then declined in wet seres (Otto et al. 2006). It seems to be a general pattern for extreme vs. moderate site conditions (Peet 1978, Osbornová et al. 1990). Macroclimate determined physiognomy of vegetation and participation of life forms in some studies (Prach 1994, Otto et al. 2006). A study of vegetation succession in 56 disused basalt quarries over a distance of 90 km, where mean annual precipitation varied between 460 and 820 mm, and mean annual temperature between 6.1 and 9.0 °C, found both these variables to be significantly correlated with vegetation pattern (Novák & Prach 2003). Besides the expected direct effects on species establishment, macroclimate influences vegetation succession through the regional species pool (Settele et al. 1996).

Substratum quality

The type of substratum is often reported to determine the course of succession; soil type is important in abandoned fields (Smit & Olff 1998; Gallego Fernández et al. 2004) and substratum texture in industrial and mining deposits (Molyneux 1963; Vaňková & Kovář 2004). Soil moisture (partly influenced by climatic factors), soil nutrients (especially nitrogen), and soil pH are often related to the type of substratum. These factors play a decisive role in driving succession at the local scale (Wilson & Tilman 2002) and often create gradients over large geographical scales (Ellenberg 1988). However, their influence on succession was not often investigated at these scales.

Soil moisture is probably the most important site factor driving succession, but it is difficult to measure it in a comparative way over a large geographical area due to local differences in actual precipitation. Moreover, precipitation itself cannot be always used as a surrogate for site moisture due to topography (but see Otto et al. 2006). Thus, simple categories evaluating site moisture can be used, such as dry, mesic, and wet (Osbornová et al. 1990, Prach et al. 2007). This robust approach may be sufficient even in tentative predictions of succession in landscape or regional scales (Prach et al. 1999). Site moisture often determines participation of different life forms and thus physiognomy of seral stages (Walker & del Moral 2003). This is evident in the participation of woody species, which is usually high in mesic sites but restricted at dry or wet extremes of the moisture gradient (Osbornová et al. 1990, Lichter 1998, Řehounková & Prach 2006)

Substratum pH exhibited significant influence in a half of the cases listed in Table 2, mostly in those that included a broad range of this factor. Both low (Schulz &Wiegleb 2000) and high (Vaňková & Kovář 2004) pH decreased species diversity and slowed down the rate of succession in various industrial and mining deposits. Low pH about 3.5 inhibited colonization by plants in some spoil heaps from brown-coal mining (Schulz &Wiegleb 2000). In an analysis of 15 successional seres on a national scale in the Czech Republic, soil pH was the only significant predictor of successional pattern among 10 soil characteristics tested (K. Prach et al., unpublished).

Amount of nitrogen exhibited significant influence in nearly all studies in which it was tested. High levels of nitrogen usually support competitive herb and grass species (Tilman 1988) which often retard the establishment of woody species (Prach & Pyšek 1994; Smit & Olff 1998).

A study comparing seres running in various habitats: a promising approach

Most of the above-mentioned studies dealt with one type of succession. We have recently developed an approach comparing a number of seres running in various human-disturbed sites over a large region (Prach et al. 2001). Sampling the 15 seres included in the same way enabled a direct robust comparison using rigorous statistics. Multivariate methods revealed that (i) species number and rate of species turnover were positively correlated with soil pH and mean annual temperature, while negatively with altitude and precipitation, and (ii) cover of woody species increased with altitude and precipitation. Thus, soil pH and macroclimate were the most important driving variables in this study (K. Prach et al., unpublished).

Future perspectives

A rigorous comparison of exact data on the course of succession, obtained in many particular sites spread over a broader geographical scale, can help to distinguish between specific and general patterns. It can thus improve successional theory which concerns broad-scale phenomena mostly on intuitive basis only (Walker & del Moral 2003, van der Maarel 2005). The broad-scale approach can help to answer some questions better than detailed local studies. The questions concern especially the differences in the course of succession along large environmental gradients, including climatic ones, divergence vs. convergence, and the influence of different land use and vegetation history. The broad-scale approach may be helpful in studying the expected influence of global change on vegetation pattern (Morecroft et al. 2004).

Because it is practically impossible, in a broad-scale study, to ensure comparativeness among distant sampling sites, this must be at least partly compensated by a high number of such sites, similarly as in traditional phytosociology. The most suitable for such broad-scale studies are abandoned fields that occur in various longitude, latitude and altitudes, and are less heterogeneous than, for example, various mining sites. Thus, using a standardized sampling seems to be easier. Combination of permanent plots and space-for-time substitution (Pickett 1989) is a reasonable approach. As promising, we see the approach when the same local experiments are repeated on a large geographical scale as have been already conducted in some EU projects (van der Putten et al. 2000).

Beside potential contribution to successional theory, knowledge on variability of spontaneous succession over a landscape scale can provide a useful framework to particular restoration projects, if they rely upon spontaneous succession or expect to manipulate the spontaneous development (Luken 1990, Klötzli & Grootjans 2001). For detailed predictions of participation of particular species in succession in a disturbed site we usually need at least a pilot study conducted just in a site, because the high stochasticity and thus often low predictability of species composition in a concrete site (Glenn-Lewin et al. 1992). Very important for restoration practice is to consider the landscape context, regarding especially sources of diaspores of desirable (target), and undesirable (e.g. invasive aliens) species and their chance to establish. Using a broad-scale experience with succession, we can tentatively predict the rate and directions of succession unless a detailed study is conducted usually due to the lack of time or money or both. Various expert systems, which can combine exact detailed data with experiential, often only qualitative knowledge, may be useful in such predictions. The model TELSA was developed to predict vegetation changes in large landscape units (Kurz et al. 2000). By the expert system SUCCESS we can tentatively predict succession in various disturbed sites in the territory of the Czech Republic (Prach et al. 1999). The large-scale approach may be practically exploited in landscape planning strategy. Because of both theoretical and practical contributions, the large-scale approach will probably receive more attention in the future studies on succession.

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Souhrn

V článku jsou shrnuty studie (37), které se zabývají sukcesí vegetace v širším krajinném měřítku (tab. 1). Studie byly vybírány podle následujících kritérií: Všechny sukcesní série začínaly na holém substrátu, bylo studováno alespoň 6 rozdílných sukcesních stadií (lokalit) a ty se nacházely na ploše alespoň 10 km^2. Zároveň v nich byl hodnocen vliv faktorů prostředí na vegetaci (nikoliv jen jejich změna během sukcese). Rozlišeny byly případy, kdy vliv faktorů prostředí na vegetaci byl statisticky testován, ať pomocí jednorozměrné nebo mnohorozměrné statistiky. Výsledky jsou shrnuty v tab. 2. Vedle očekávaného vlivu času měly nejčastěji signifikantní vliv na průběh sukcese tyto faktory: okolní vegetace, makroklima, půdní vlhkost, obsah dusíku v substrátu a struktura substrátu. Méně častý byl signifikantní vliv velikosti narušeného místa, pH a obsahu organické hmoty a fosforu v půdě. Okolní vegetace měla vliv na průběh sukcese vždy, když byla testována. Z toho vyplývá, že sukcese na konkrétním místě by neměla být studována a interpretována bez krajinného kontextu. Studium sukcese vegetace v širších geografických rozměrech může přispět jak k teorii ekologické sukcese, tak k aplikacím poznatků především v ekologii obnovy narušených míst.

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