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Patch dynamics and local succession in a sandstone area with frequent disturbance

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Abstract. A system of sand talus cones in a small forested rocky sandstone area was investigated to determine the importance of disturbance-related dynamics and mesoclimate to vegetation differentiation. These cones (usually 3-12 m long) are formed by the accumulation of sand at the foot of sandstone rocks and are subject to frequent disturbance by the transport of sand. Vegetation was recorded both at the whole-cone level and at the within-cone level; the latter was approached by means of a transect of small squares along each cone. Soil profiles were recorded at the upper, centre and bottom parts of the cones. To express mesoclimatic differentiation among the cones within the rocky area, the potential insolation was calculated from the horizon angular height and the likelihood of thermal inversions was estimated by the height of the cones above the valley bottom.

The major environmental factor correlated with variation in cone vegetation is the disturbance dynamics as determined by the structure of the soil profile; active cones (with sand at the surface) are colonized by different species as compared with non-active cones (with surface covered by humus sediments). There is a clear primary succession gradient from plants able to cope with continuous sand transport to stands of tall bryophytes, small shrubs and herbs. Quite often the same gradient is found within cones, with late successional vegetation confined to the lower, stabilized parts of the cones, while the upper part is still being affected by sand transport. The differentiation along the gradient of disturbance is much stronger than the differentiation due to climatic or other gradients.

Indirect data indicate that the long-term average rate of sand accumulation is ca. 1 mm/yr. If sand transport ceases, *Sphagnum* peat accumulates on some of the cones; the depth of accumulated *Sphagnum* remains may reach 50 cm. The development of the peat layer is but weakly correlated with the measured variables suggesting that random processes at the beginning of *Sphagnum* establishment may be a driving force. By measuring *Sphagnum* growth and decomposition, and the peat density, we estimated the time needed for their development to be several hundreds of years.

Keywords: Bryophyte; DCA; Microclimate; Peat decomposition; Sand accumulation; *Sphagnum* growth; Talus cone.

Nomenclature: Tutin et al. (1964-1980) for vascular plants; Frey et al. (1995) for bryophytes .

Introduction

Disturbance has been shown to maintain species richness both by theoretical modelling (Huston 1979; see also Wilkinson 1999) and by empirical data (Kimmerer & Allen 1982; Pickett & White 1985; for a review see van der Maarel 1993). As a process, disturbance can be considered as being external to the system, generated by various (mainly physical) factors that reset the successional stage of vegetation at the site. A landscape with frequent disturbances then becomes a patchy mosaic of differently aged successional stands with their own dynamics (Pickett 1980). The size of these stands is essentially a function of the disturbance grain; the distribution of their successional ages is a function of the disturbance frequency (Pickett 1980; Palmer 1994). Such systems often develop where there is enough external energy available to cause frequent disturbance, such as at sea shores, river banks, regions with strong geomorphological differentiation etc. The vegetation of such systems is often specifically determined by the disturbance regime (Kimmerer & Allen 1982; Meyer et al. 1992; Friedman et al. 1996; Bornette & Amoros 1996; Sakio 1997).

Disturbance is best studied using permanent plots, in which the development after natural or experimentally induced disturbance can be followed; however, plot size and observation time span have to be commensurate with the disturbance regime. Since disturbance acts at very different temporal and spatial scales, from centimetres to tens or hundreds of kilometres, it is often rather difficult to demonstrate its action directly within realistic time and space frames for permanent plot studies, especially for broad-scale and/or infrequent disturbances. Then indirect means have to be used to infer time since the last disturbance event (Pickett 1989). For systems with erosion/sedimentation dynamics, the sediment structure may contain a good record of the past history (Embleton & Thornes 1979). Easily weathered bedrocks are prime cases where this approach could be used for finer time scales. In the current paper we apply this approach to sandy sediments in a region of Cretaceous sandstones in the Czech Republic.

Cretaceous sandstones form landscapes with extreme geomorphological gradients and continuous strong erosion processes. This is due to the water permeability of sandstones, which reduces horizontal water run-off and enables the formation of deep erosion canyons. Due to the relative ease of sandstone weathering, rocks at these canyons are subject to intensive denudation and various erosion structures form at, and close to, their bottoms (Balatka & Sládek 1984). A broken surface relief gives rise to a strong mesoclimatic differentiation within sandstone regions, with dry and warm plateaus and damp and cool canyon bottoms.

Among the many erosion/sedimentation structures in the canyons, sand talus cones are the most regularly and recurrently occurring structures. They are formed at sedimentation sites below rocks, or in erosion furrows on valley bottoms or on rock terraces (Rubín et al. 1986). They are rather steep, half-cone shaped, the slopes usually ranging between 20-40 °, and their lengths vary from 3 to 12 m. No rock fragments are formed during sandstone weathering which can slow down the erosion rates (Simanton et al. 1994); therefore the sand is freely transported along the slope to form these typical cone-shaped structures. The major source of disturbance in the sand cones is transport of sand from erosion/sedimentation processes in ‘embryonic’ canyons close to the upper point of the cone; bursts of sand sedimentation are often due to sudden movements of the rock blocks above the cone. Consequently, sand input is hardly affected by the vegetation at the cone. The disturbance includes both denudation and accumulation, though accumulation largely prevails. This offers a remarkable system characterized by disturbance dynamics. Since the talus sediment can easily be excavated, the history of their development and the currently active processes (sand sedimentation, humus accumulation, and/or *Sphagnum* peat growth) can be easily identified. Thus, the disturbance dynamics at each site can be inferred. The within-cone heterogeneity of the sediment structure (upper vs. lower parts) enables determination of recent sedimentation and its spatial scale (whether it extends over the whole cone, or whether it is limited to the upper part only).

The vegetation of sand talus cones shows remarkable differentiation, ranging from sparse bryophyte and grass cover to thick cover of large mosses and ericaceous shrubs (Herben 1992). Some cones bear vegetation with dominant *Sphagnum* and are subject to accumulation of peat. The first aim of this study is to determine whether the major factor determining the cone vegetation is the disturbance dynamics or if some other factor, such as mesoclimate, is more important.

Secondly, since the cones are heterogeneous – due to spatially restricted sand transport – and often have different vegetation in the upper and lower parts, we attempted to identify the rules for this internal structure and to relate them to the disturbance gradients.

Thirdly, we attempted to link the peat accumulation at the cones with the disturbance dynamics, and to identify the disturbance and climatic conditions that are correlated with high likelihood of peat formation. Further, we determined the rate of peat accumulation by measuring growth and decomposition of the *Sphagnum* peat and to compare it with rates of sand sedimentation.

Methods

Study site

Cretaceous sandstones are rather common in the triangle formed by the Czech Republic, Germany and Poland. This research was carried out in the area of the Adršpach-Teplice Rocks (Adršpašsko-teplické skály), the sandstone area with the highest altitudinal range in the whole region. It lies in the northern part of the Czech Republic (16° 05' - 16° 10' E, 50° 33' - 50° 37' N) and covers an area of 20.5 km^2. The area itself is an isolated plateau built of uppermost Cretaceous block sandstones. The altitude of the rock summits in the area ranges from 500-600 m in the North to 600-700 m in the South; the altitudinal range is 306 m. The plateau surface is divided by numerous gorges and canyon-like valleys that follow networks of Tertiary faults (Řezáč 1955; Balatka & Sládek 1984). The depth of the canyons reaches 80-100 m, in the SE part of the area up to 180-200 m; their width ranges from several m to tens of m at the bottom and from several tens or hundreds of m at the tops. The substratum is very poor in nutrients; more than 99% of the rock material is silicium dioxide (Řezáč 1955).

The mean temperature of the coldest month (January) is –3 - – 4 °C, the mean temperature of the warmest month (June) is 15-17 °C, and the mean yearly temperature is 6°C (Vesecký et al. 1958). Mean yearly precipitation is 700-1000 mm with a maximum in July and a minimum in February (Vesecký et al. 1958). However, the climatic conditions in the narrow valleys and canyons are much wetter and colder due to frequent thermal inversions (Zittová-Kurková 1984; Hadač & Sýkora 1984). This is also indicated by the occurrence of subalpine species (e.g. *Athyrium distentifolium*, *Empetrum nigrum* ssp. *hermaphroditum*, *Polytrichum alpinum*, *Dicranodontium asperulum*, *Pohlia drummondii*) and species with a (sub-)oceanic distribution (e.g. *Galium saxatile*, *Blechnum spicant*, *Kurzia sylvatica*, *Tetrodontium repandum*, *Plagiothecium undulatum*).

Most of the area is covered by forests. Palynological records show a great importance of broad-leaved trees (*Acer* spp., *Fagus sylvatica*) in the Subatlantic period after 2500 BP (Chaloupková 1995; Jankovská unpubl.); currently, however, most of the region is covered by Norway spruce (*Picea abies*).

Data collection

All talus cones in three selected subregions within the Adršpach-Teplice Rocks that satisfied the following criteria were sampled. The cones had to have (1) one predominant and clearly defined source of sand and (2) morphologically well developed margins (flanks and bottom). Altogether 155 talus cones were sampled. The structure and vegetation of each sand talus cone was described by recording the following variables (see Table 1).

Physical variables of the talus cone. Two cone size variables were recorded by a measuring tape: length (from the top to the cone base) and width (recorded at the cone base). The azimuth angle of the cone was measured in the direction of the baseline at the cone centre. using a geological compass. Further, inclination (using a clinometer) and sediment type and depth were measured at three positions along the baseline: 1 m from the top (referred to as upper position), centre (referred to as central position) and 1 m from the base (referred to as basal position). Sediments were classified into substrate types that could be easily recognized in the field: humus layer, *Sphagnum* peat, sand (including sand mixed with organic material). Some soil data are missing for six cones.

Position of the talus cone in the valley. First, altitude of the cone and the altitude of the bottom of the canyon at which the cone is situated were measured by an altimeter with a precision of 3 m. The relative height was expressed as the difference between these two altitudes. This variable indicates the likelihood and/or intensity of temperature inversions. Furthermore, the angular height of the horizon at eight cardinal points (N, NW, W, SW, S, SE, E, NE), was measured at the centre of each cone using a geological compass. Potential direct solar irradiation (PDSI) was calculated for each talus from data on exposition, slope and angular height of the horizon at these cardinal points following Jeník & Rejmánek (1969). The potential solar radiation was expressed in relative terms, i.e. as sums of cosines of angles at which the solar radiation reaches the surface, summed over the period when the sun is above the horizon at that particular cone. The potential solar radiation was expressed as monthly sums beginning with January (21 Dec to 20 Jan) to June (21 May to 20 June); the values for the second part of the year were not calculated because they almost perfectly mirror the first part.

Presence of all vascular plants and bryophytes were recorded on the whole talus cone. The overall cover of each species was assessed by the 7-degree Braun-Blanquet scale (Ellenberg & Mueller-Dombois 1974). The vertical projection of the cover of the tree layer (if any) was recorded, no matter whether the trees were rooted at the cone or not.

To account for the within-cone heterogeneity, a vertical transect line was established on each cone. Presence/absence of all vascular plants and bryophytes was recorded in small plots of 20 cm × 20 cm, established along the baseline at 1 m intervals. Depending on the cone length, there were 3 to 12 small plots along the transect; altogether 758 small plots were recorded. These plots are further referred to as ‘small plots’.

Table 1. List of cone variables used in the analyses. c = continuous variable, d = categorical variable (number of states in parentheses).

Code	Type	Description
Structural variables		
Slope upper/centre/bottom	c	Slope at the upper position of the cone /in the cone centre/at the basal position of the cone
Substratum upper/centre/bottom	d (3)	Substratum type (sand, humus or layered) at the upper position of the cone/in the cone centre/at the basal position of the cone
Length	c	Cone length
Width	c	Cone width
Position variables		
Height	c	Height of the cone above the valley bottom
Potential radiation	c	Sum of direct potential radiation in individual months (January to June)

Data analysis: entire cones

The vegetation of entire cones was summarized using Detrended Correspondence Analysis (DCA; Hill 1979a) with detrending by segments and downweighting of rare species. All calculations were done using the program CANOCO version 4.0 (ter Braak & Šmilauer 1998). Separate DCA ordinations were made for floristic lists from the cones (presence/absence data) and for the cover values transformed using the van der Maarel transformation (van der Maarel 1979). Since there was little difference between the two, only results obtained by use of qualitative data are presented here. The principal DCA axes were further correlated with the environmental variables measured at the cones. The following variables were used: (1) variables describing the structure of the cone (further referred to as *structural variables*). These were the length and width of the cone and inclination and sediment type and depth at upper, central and basal positions. (2) variables describing the position and potential radiation regime of the cone (further referred to as *position variables*, since the potential solar radiation and microclimate regime are primarily determined by the position of the cone within the canyon). These were: monthly sums of the potential radiation (see above), and relative height above the bottom of the valley.

Data analysis: small plots within cones

The data on small 20 cm × 20 cm squares collected along the transects within cones were used to assess the within-cone heterogeneity. The vegetation of small plots was classified by TWINSPAN (Hill 1979b) based on qualitative data (i.e. with no pseudospecies cut levels and with minimum group size for division of six). All small plots of all transects were classified in one analysis. A classification technique (TWINSPAN) was used instead of ordination due to the low number of species present in some of these plots (ordination methodology generally works poorly with very sparse data sets; Økland 1990); in addition, the approach based on classification made possible to take account of the plots with no species recorded. The TWINSPAN groups were tested for non-randomness of occurrence with respect to (1) botanical composition of the entire cones at which they occur (identified by the positions of DCA axes of entire cones) and (2) positions within cones (upper part, centre, basal part). Each TWINSPAN group was tested separately by a stepwise logistic regression with presence of the group tested as the dependent variable and position and DCA axes scores as explanatory variables; effects of interactions were also tested in a stepwise manner after the main effects had been accounted for. Position within the cone was taken as a categorical variable with three levels (upper part, centre, basal part). The calculations were done using BMDP program LR with log-likelihood ratio difference (with $P = 0.05$ threshold) as the criterion for the inclusion of the effect into the model (Dixon et al. 1990).

Environmental factors associated with peat development were also tested using logistic regression with peat development as the dependent variable and position and structural variables of the cones as explanatory variables.

Measurement of Sphagnum growth and decomposition

26 cones with high cover (> 50% at an area of at least 1m^2) *Sphagnum* (*S. capillifolium, S. girgensohnii* or *S. quinquefarium*) growth were selected using a stratified random approach. At each of the sites, six randomly selected *Sphagnum* plants were marked by a coloured thread at a distance ca. 1 cm below the capitulum of the plant in May 1989. The increase in the distance between the coloured thread and the capitulum of the plant was measured in August 1989, May 1990, October 1990 and May 1991. No reduction of head growth or survival was observable during the study period. In May 1991, the number of capitula were counted at each site over an area of 10 cm × 10 cm and the plants were harvested. 10 plants from each site were cut to a length of 4 cm from the top of the capitulum and then the capitulum (length 1 cm from the top) was removed. These plants were dried to constant weight at 90 °C and weighed; the resulting figure was recalculated to mean length-specific mass of *Sphagnum* plant (g/cm length). This value was used to calibrate the yearly increments in length and to estimate biomass production per area using the density figures for each site. In the sloping *Sphagnum* carpets the current method of measuring individual plants is preferable to measurement of whole-carpet growth (as used e.g. by Lindholm & Vasander 1990; Rochefort et al. 1990), since individual plants do not grow vertically (for discussion of different techniques see Clymo 1970).

To measure decomposition of *Sphagnum* biomass, plastic mesh bags (mesh size 1.5 mm) with 3 g of green *Sphagnum girgensohnii* mass were buried to a depth of ca. 10 cm in three different cones in autumn 1988. Five bags were removed from each site at yearly intervals from 1989 to 1993. The contents of the bags were dried to constant weight and weighed; the inorganic matter content was determined by dry mineralization at 550 °C. The net organic matter was determined as the mass of the bag content minus the mass of the inorganic matter.

The density of the *Sphagnum* peat was determined by taking 70 cm^3 using a sampler designed to keep the soil structure intact. The samples were taken from three different cones with peat from a depth of 5-10 cm from the surface of the peat sediment. These samples were dried to constant weight. The net organic matter was determined as the mass of the sample dry mass minus the mass of the inorganic matter; the latter was determined by mineralization at 550 °C.

Results

Cone physical structure

The cones had a characteristic structure. They generally consisted of sand, with or without overlay of accumulated humus layers of variable thickness. Bare sand sediments (not covered with humus) occurred in upper positions of the cones much more often than in basal positions, while cones with humus in upper positions and with sand in basal positions are quite rare (Table 2). There was a pronounced correlation pattern within the set of structural variables (Table 3). Slopes at all three cone positions are correlated (Pearson correlation coefficients range between 0.26 and 0.39; all values significant at $P < 0.001$; Table 3). Slopes are negatively correlated with cone size variables (bigger cones are less sloping; the correlation coefficient of cone width and slope range between 0.16 an 0.2). Bigger cones are more likely to have humus sediment at the bottom part than small cones. There are also some significant relationships between cone structure and cone position in the valley: typically, cones at valley bottoms are less sloping.

Vegetation of the cones and environment relations

The first two DCA axes had eigenvalues of 0.176 and 0.107, and gradient lengths of 2.104 and 1.719. In terms of species composition, the first axis separates species of humus-covered cones (e.g. *Hylocomium splendens, Pleurozium schreberi, Pinus sylvestris, Cynodontium* spec., *Cladonia* spec., *Leucobryum juniperoideum*; cf. Fig. 1) from species growing primarily on active sand (e.g. *Calypogeia azurea, C. integristipula, Deschampsia flexuosa, Polytrichum* spp., *Mylia taylori, Mnium hornum*).

Many environmental variables were significantly correlated with the floristic composition of the cones as expressed by the scores along the two first DCA axes (Table 3). Most of the correlations were with the structural variables. The first axis was strongly negatively correlated with presence of humus in upper, central and bottom parts, positively with the presence of sand, and negatively with the slope of the cone in the upper and central parts of the cones. The second axis was correlated with the slope in the upper part and with potential direct radiation in all six periods tested.

Table 2. Frequency of different types of spatial arrangement of sediment within cones. S = sand (including layered sand), H = organic sediment (humus).

	Sediment type at the surface							
Upper part	S	S	S	S	H	H	H	H
Central part	S	S	H	H	S	S	H	H
Bottom part	S	H	S	H	S	H	S	H
Number of cones	14	24	7	49	3	4	1	47

Existence of a peat layer (either living or buried) was independent of recorded factors of the environment (structural and position variables of the cones). The only significant predictor of presence of a peat layer, using logistic regression, was slope in the upper part of the cone ($\chi^2 = 11.13$, $P = 0.001$).

Vegetation structure within individual cones

The TWINSPAN classification of small 20cm × 20cm plots yielded a clearly interpretable structure at the level of 10 classes (Table 4); plots without vegetation are treated as the 11th class. The relative floristic poverty of the small plots lead to formation of groups characterized by a few very frequent (and often dominant) species.

Individual groups from this classification tended to be associated with specific positions within the cones (Table 4). For example, small plots of class S1 (no vegetation), S10 (with small hepatics) and S11 (with high frequency of *Dicranodontium denudatum* and *Mylia taylori*) occurred more often in the upper parts of the cones more likely to be affected by disturbance. Class S2 (with high frequency of *Vaccinium vitis-idaea*), S5 (with *Vaccinium myrtillus* and large bryophytes), S7 (with *Sphagnum* and *Polytrichum*) predominantly occurred in the lower parts of the cones.

In addition, there was a clear relationship between the occurrence of TWINSPAN groups of small plots at individual cones and the position of these cones in the DCA ordination (Table 4). In particular, types S6, S7, and S8 occurred on cones with a high score on the first axis, i.e. those associated with more disturbed cones. On the other hand, types S1, S2 and S9 are associated with less disturbed cones. The interaction between position and DCA axis was never significant; this indicates that if an individual species group occupies a specific position at the cone, this position is the same

Table 3. Pairwise correlations among environmental variables and between environmental variables and the first two DCA axes. The values in the triangle below the main diagonal is the Kendall correlation coefficient; values above the main diagonal are associated untransformed type I error probability. Values indicated in bold are significant at this level. (For the DCA axes correlations, the type I error probabilities are in the line below the correlation coefficients.) For the number of tests between DCA axes and environmental variables, the Bonferroni corrected significance level ($P = 0.05$) is 0.0011; for all tests in the table, the Bonferroni corrected significance level ($P = 0.05$) is 0.0002. For variable definitions, see Table 1. The three-state categorical variables were recoded as three two-state variables to better portray their correlations with the axes; as a result, pairwise correlations between these variables cannot be tested and are not reported.

	Length	L-U	H-U	S-U	L-C	H-C	S-C	L-B	H-B	S-B	Width	Slope-U	Slope-C	Slope-B	Height	Jan	Feb	Mar	Apr	May	Jun
Length	.	0.417	0.099	0.058	0.043	0.737	0.115	0.776	0.029	0.013	<0.001	0.369	0.808	0.11	0.173	0.118	0.005	0.012	0.011	0.006	0.009
Layered-upper	–0.055	.			0.164	0.063	0.239	0.002	0.11	0.475	0.635	0.435	0.879	0.226	0.837	0.814	0.696	0.954	0.873	0.982	0.757
Humus-upper	–0.111		.		0.95	0.001	<0.001	0.77	0.041	0.022	0.484	0.012	0.794	0.573	0.01	0.353	0.351	0.313	0.287	0.27	0.379
Sand-upper	0.127			.	0.695	0.008	0.002	0.457	0.135	0.012	0.397	0.006	0.758	0.34	0.009	0.32	0.294	0.31	0.318	0.28	0.332
Layered-centre	**0.136**	0.113	–0.005	–0.032	.			0.013	0.466	0.225	0.113	0.645	0.641	0.954	0.464	0.228	0.566	0.067	0.09	0.081	0.561
Humus-centre	0.023	–0.151	**0.268**	**–0.216**		.		0.043	<0.001	<0.001	0.805	0.399	0.193	0.146	0.977	0.474	0.733	0.792	0.715	0.74	0.749
Sand-centre	–0.106	0.095	**–0.286**	**0.252**			.	0.479	<0.001	<0.001	0.495	0.233	0.091	0.108	0.639	0.958	0.477	0.419	0.536	0.494	0.489
Layered-bottom	–0.019	**0.257**	–0.024	–0.06	**0.201**	**–0.164**	0.057	.			0.676	0.624	0.3	0.719	0.862	0.221	0.383	0.387	0.515	0.4	0.358
Humus-bottom	**0.146**	–0.13	**0.166**	–0.121	–0.059	**0.419**	**–0.417**		.		0.525	0.637	0.719	0.555	0.328	0.273	0.249	0.264	0.266	0.264	0.282
Sand-bottom	**–0.166**	–0.058	**–0.186**	**0.203**	–0.098	**–0.381**	**0.471**			.	0.663	0.326	0.682	0.307	0.284	0.749	0.488	0.514	0.406	0.501	0.578
Width	**0.395**	–0.032	–0.047	0.057	0.107	–0.017	–0.046	–0.028	0.043	–0.029	.	0.006	0.099	0.002	0.065	0.089	0.004	0.007	0.005	0.003	0.005
Slope-above	–0.052	0.054	**0.174**	**–0.19**	0.032	0.059	–0.083	0.034	0.033	–0.068	**–0.159**	.	0.01	0.001	0.045	0.01	0.03	0.154	0.187	0.199	0.046
Slope-centre	–0.014	0.011	0.018	–0.022	–0.033	–0.092	0.119	–0.073	0.025	0.029	–0.096	**0.153**	.	0.001	0.01	0.101	0.043	0.049	0.054	0.049	0.031
Slope-bottom	–0.092	0.084	0.039	–0.066	–0.004	–0.101	0.112	–0.025	–0.041	0.071	**–0.174**	**0.203**	**0.206**	.	0.002	0.025	0.014	0.019	0.049	0.025	0.02
Height	0.076	0.014	**0.176**	**–0.178**	0.05	0.002	–0.032	–0.012	0.066	–0.073	–0.103	**0.117**	**0.151**	**0.185**	.	0.619	0.809	0.866	0.872	0.999	0.695
PDSI-January	0.09	–0.017	–0.065	0.07	–0.084	0.05	–0.004	–0.086	0.077	–0.022	0.098	**–0.154**	0.099	**–0.133**	–0.029	.	<0.001	<0.001	<0.001	<0.001	<0.001
PDSI-February	**0.157**	–0.026	–0.063	0.071	0.039	0.023	–0.048	–0.059	0.078	–0.047	**0.158**	**–0.125**	**0.118**	**–0.142**	0.014	**0.701**	.	<0.001	<0.001	<0.001	<0.001
PDSI-March	**0.138**	–0.004	–0.067	0.068	**0.122**	–0.018	–0.054	–0.058	0.075	–0.044	**0.148**	–0.081	**0.114**	**–0.134**	–0.009	**0.551**	**0.786**	.	<0.001	<0.001	<0.001
PDSI-April	**0.14**	0.011	–0.071	0.066	**0.113**	–0.024	–0.041	–0.043	0.074	–0.055	**0.154**	–0.075	0.111	**–0.112**	–0.009	**0.505**	0.726	**0.882**	.	<0.001	<0.001
PDSI-May	**0.151**	0.002	–0.073	0.072	0.116	–0.022	–0.046	–0.056	0.074	–0.045	**0.162**	–0.073	0.113	**–0.128**	<0.001	**0.539**	**0.772**	**0.966**	**0.902**	.	<0.001
PDSI-June	**0.144**	–0.021	–0.059	0.065	0.039	0.022	–0.047	–0.062	0.072	–0.037	**0.154**	**–0.115**	**0.126**	**–0.134**	0.022	**0.695**	**0.972**	**0.787**	**0.735**	**0.773**	.
DCA Axis 1	0.002	0.019	**–0.258**	**0.249**	–0.013	**–0.189**	**0.211**	0.097	**–0.202**	**0.169**	–0.028	**–0.278**	**–0.217**	–0.068	–0.104	0.001	–0.062	–0.1	–0.103	–0.101	–0.068
Signif.	0.967	0.775	<0.001	<0.001	0.849	0.005	0.001	0.145	0.002	0.011	0.605	<0.001	<0.001	0.235	0.061	0.991	0.258	0.066	0.059	0.063	0.217
DCA Axis 2	**0.139**	–0.06	–0.055	0.074	0.111	–0.017	–0.048	–0.093	0.045	0.024	0.09	**–0.221**	0.046	0.01	0.005	**0.125**	**0.122**	**0.133**	**0.133**	**0.136**	**0.117**
Signif	0.011	0.366	0.407	0.266	0.096	0.799	0.47	0.16	0.503	0.715	0.101	<0.001	0.421	0.864	0.93	0.028	0.027	0.014	0.014	0.012	0.032

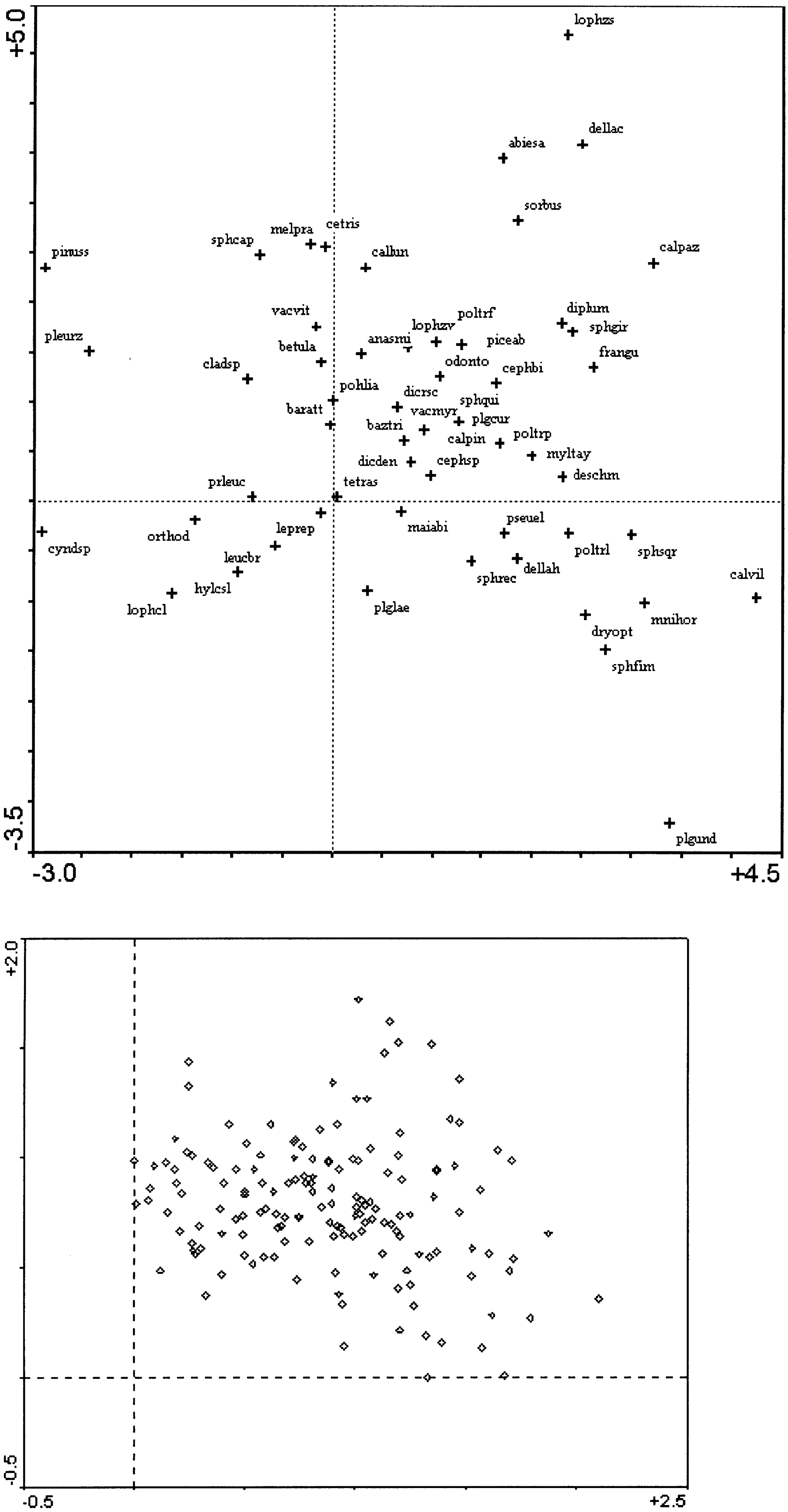

Fig. 1. Ordination of cones by Detrended Correspondence Analysis based on presence/absence data; (**a**) species scores, (**b**) stand (cone) scores. Only species recorded more than once are shown.
abiesa = *Abies alba*; anasmi = *Anastrophyllum minutum*; baratt = *Barbilophozia attenuata*; baztri = *Bazzania trilobata*; betula = *Betula* spp.; callun = *Calluna vulgaris*; calpaz = *Calypogeia azurea*; calpin = *Calypogeia integristipula*; calvil = *Calamagrostis villosa*; cephbi = *Cephalozia bicuspidata*; cephsp = *Cephalozia* spec.; cetris = *Cetraria islandica*; cladsp = *Cladonia* spp.; cyndsp. = *Cynodontium* spec.; dellac = *Dicranella cerviculata*; dellah = *Dicranella heteromalla*; deschm = *Deschampsia flexuosa*; dicden = *Dicranodonotium denudatum*; dicrsc = *Dicranum scoparium*; diplum = *Diplophyllum albicans*; dryopt = *Dryopteris* spp.; frangu = *Frangula alnus*; hylcsl = *Hylocomium splendens*; leprep = *Lepidozia reptans*; leucbr = *Leucobryum juniperoideum*; lophcl = *Lophocolea* spp.; lophzs = *Lophozia sudetica*; lophzv = *Lophozia ventricosa*; maiabi = *Maianthemum bifolium*; melpra = *Melampyrum pratense*; mnihor = *Mnium hornum*; myltay = *Mylia taylorii*; odonto = *Odontoschisma denudatum*; orthod = *Orthodontium lineare*; piceab = *Picea abies*; pinuss = *Pinus sylvestris*; pleurz = *Pleurozium schreberi*; plgcur = *Plagiothecium curvifolium*; plglae = *Plagiothecium laetum*; plgund = *Plagiothecium undulatum*; pohlia = *Pohlia nutans*; poltrf = *Polytrichum formosum*; poltrl = *Polytrichum longisetum*; poltrp = *Polytrichum pallidisetum*; prleuc = *Paraleucobryum longifolium*; pseuel = *Pseudotaxiphyllum elegans*; sorbus = *Sorbus aucuparia*; sphcap = *Sphagnum capillifolium*; sphfim = *Sphagnum fimbriatum*; sphgir = *Sphagnum girgensohnii*; sphqui = *Sphagnum quinquefarium*; sphsqr = *Sphagnum squarrosum*; tetras = *Tetraphis pellucida*; vacmyr = *Vaccinium myrtillus*; vacvit = *Vaccinium vitis-idaea*.

Table 4. TWINSPAN classification of 20 cm × 20 cm plots, frequency of their occurrence in the upper, central and bottom parts of the cones. Species with frequency > 20% in the classes are shown; species occurring in more than 50% of the plots in the particular class are given in bold. Occurrence of small plots classes at different positions within the cone and at different cone types was tested using stepwise logistic regression with position and DCA axes scores as explanatory variables. The table lists a log-likelihood ratio difference for each effect at the step when it was included. Sign of the regression coefficient for linear effects is given in brackets. The $P = 0.05$ threshold of the log-likelihood ratio difference was used to stop the analysis. N/A, no test performed due to low number of occurrences. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. No interaction between position and axis was significant. sed. = sedimentation.

Class	Species	Ecology	Upper	Central	Bottom	Axis 1	Axis 2	Position code
S1	No vegetation	Often sand sed.	40	17	7	(–) 21.57***		5.32*
S2	*Vaccinium myrtillus*, ***Vaccinium vitis-idaea***, ***Dicranum scoparium***	Dry, no recent sed.	16	29	45	(–) 25.00***	(–) 12.00	12.67**
S3	***Orthodontium lineare***	Dry, no recent sed.	2	4	1	N/A	N/A	N/A
S4	***Vaccinium myrtillus***, *Dicranum scoparium*	Moderate, no recent sed.	45	83	54		(+) 9.19**	8.17*
S5	*Vaccinium myrtillus*, ***Bazzania trilobata***, *Dicranum scoparium*	Moderate, no recent sed.	11	41	39		(+) 5.70*	19.04***
S6	***Polytrichum formosum***	Recent sed.	19	30	22	(+) 47.60***		
S7	*Sphagnum quinquefarium*, *Deschampsia flexuosa*, ***Polytrichum formosum***,***Vaccinium myrtillus***	Wet, often recent sed.	19	48	54	(+) 26.18***	(+) 4.57*	14.29***
S8	***Polytrichum longisetum***, *Dryopteris* spec.	Wet	6	6	5	(+) 19.46***		
S9	***Leucobryum juniperoideum***, *Tetraphis pellucida*	Wet, no recent sed.	10	13	11	(–) 32.34***	(–) 7.84**	
S10	*Bazzania trilobata*, *Pohlia nutans*, *Lepidozia reptans*, ***Calypogeia integristipula***	Wet, sand sed. in the past	31	30	19		(–) 11.18***	
S11	*Mylia taylori*, *Calypogeia integristipula*, ***Dicranodontium denudatum***	Wet, current sand sed.	27	22	18			

irrespective of the other vegetation or environmental conditions of the cone.

Sphagnum growth and decomposition

Mean yearly increments in length ranged from 2.5 mm/yr to 55.9 mm/yr with means of 20.2 (1989) and 16.7 (1990) (Table 5). There was much variation among individual measurement sites; a nested ANOVA (site nested within taxon) showed that this variation was highly significant in 1989, but only marginally so in 1990 and that variation among species was not significant (marginally in 1989); (taxon 1989: d.f. = 1, F = 4.09, P = 0.072; 1990: F = 0.35, P = 0.566; site 1989; d.f. = 5, F = 12.0, P < 0.001; 1990: F = 2.23, P = 0.036). The primary production per unit area estimated from mean growth rates was 0.11 $g.cm^{-2}.yr^{-1}$ (1989) and 0.09 $g.cm^{-2}.yr^{-1}$ (1990).

Table 5. Components of *Sphagnum* growth. Individual values of yearly increments are means from six stems at each site. Specific stem mass is estimated using 10 stem segments measuring 3 cm from each site. Stem density is estimated in 10 cm × 10 cm plots. n = 24 for all parameters.

	Mean	Standard error
Yearly increment 1989 [cm/yr]	2.02	0.27
Yearly increment 1990 [cm/yr]	1.67	0.20
Specific stem mass [g/cm]	0.004	0.0002
Stem density [$stems/cm^2$]	1.39	0.078
Primary production 1989 [$g.cm^{-2}.yr^{-1}$]	0.011	0.001
Primary production 1990 [$g.cm^{-2}.yr^{-1}$]	0.009	0.001

Decomposition of organic matter was fast in the first year (ca. 30% reduction in mass) and very slow later on (see Fig. 2). However, the rate of decrease over time (after the first year) was significant using analysis of covariance (sites as effects: F = 28.7, d.f. = 2,71, P < 0.0001 and time as covariate: F = 12.9, d.f. = 1,71, P = 0.0006). According to a linear model the time to full decomposition of the organic matter would be 43 yr; using an exponential model the time to decomposition to 10% of the original mass would be 86 yr. The coefficient of determination between time and decomposition was 0.0912 for the linear model and 0.0889 for the exponential model. The decrease in organic matter over time was not significant if the decrease over the first two years was excluded (sites as effects: F = 18.4, d.f. = 2,56, P < 0.0001 and time as covariate: F = 2.7, d.f. = 1,56, P = 0.11). The specific density of the organic matter in *Sphagnum* peat in the cones was 0.102 g/cm^3 (n = 15, s.e. = 0.0063).

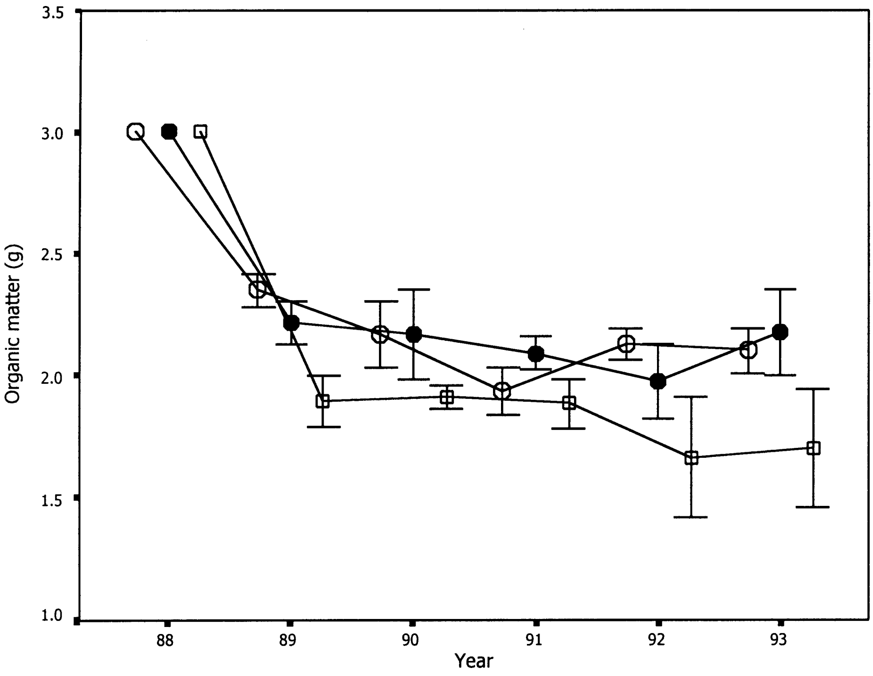

Fig. 2. Mean organic matter remaining in mesh bags exposed at three different cone sites. Points (except those for time = 0) are means from five bags.

Discussion

Major factors affecting cone vegetation

The results show that a gradient in disturbance intensity has a major effect on the vegetation of the cones. The primary variables determining cone vegetation are sediment type (both in the upper and lower parts of the cone) and slope (mainly in the upper part). Both sediment type and slope are clearly linked to the disturbance regime; the presence of a sand layer on the cone surface (or sand layered with organic material) is evidence of recent sedimentation. On the other hand, humus is transported along the cone much less easily; most stays where it is formed. The presence of humus sediments without sand is thus an indicator that no recent disturbance has occurred. There is no pronounced relation between slope and occurrence of humus. While a less inclined surface is less likely to support sand movement, many humus-covered cones with no recent sand input may have very high slopes. If a cone undergoes several cycles of sand sedimentation and humus accumulation (when no sand is transported), a layered sediment structure develops. Such cones, though not very common, do occur in the region (four cones had a layered structure in the upper parts; 11 in the basal parts).

Disturbance by sand deposition rejuvenates the site; primary succession (linked to humus accumulation and surface fixation) begins after cessation of sand transport. Time since disturbance is an important determinant of vegetation because of a pronounced ecological differentiation among species with respect to preference for successional stage. Succession on the cones begins with fast-growing bryophytes and grasses which are able to colonize bare sand; some of these species are well adapted to cope with continuous transport of sand. These are species with fast lateral growth (*Calypogeia integristipula, Lepidozia reptans, Deschampsia flexuosa, Polytrichum* spp.) and species regenerating from vegetative fragments and/or spores (*Dicranodontium denudatum, Calypogeia integristipula, Pohlia nutans*). Later, a cover of small shrubs (*Vaccinium* spp.) with common accompanying bryophytes (*Dicranum scoparium, Bazzania trilobata*) develops. Similar effects of geomorphological gradients on vegetation disturbance and succession have often been demonstrated in desert vegetation (Meyer et al. 1992; see also e.g. Embleton & Thornes 1979).

If the rate of rock weathering is low, sand sedimentation may be confined to the upper parts of the cone. Sand transport depends on a sufficient amount of run-off water (Parsons et al. 1994). Since the rates of percolation through the cones are very high due to the porous nature of the substratum, sand transport tends to cease at some point downward along the cone. This explains the prevalence of sand in the upper parts of the

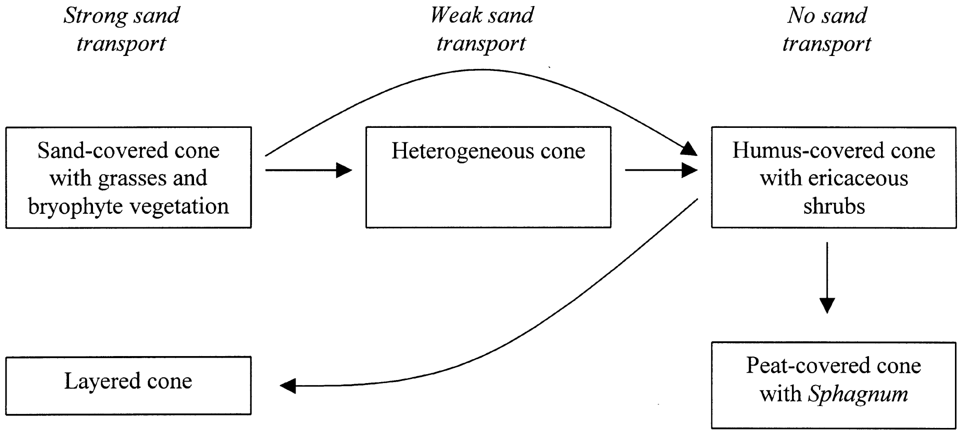

Fig. 3. Schematic representation of potential transitions between individual cone types due to changes in sand transport.

cones and the high frequency of cones with sand in the upper and humus in the basal parts (cf. Table 2). In such cones the upper part represents a younger successional stage than the lower part. Early successional species (or bare ground without vegetation) is hence likely to occur in the upper parts of the cones; later successional species (robust mosses and *Vaccinium* species) are more likely to occur at lower parts of the cones.

While it is easy to rank cones with respect to position along the disturbance gradient, the absolute time scale of the disturbance process is difficult to determine. Two sources of indirect evidence are, however, available. Firstly, in 1824 a forest fire affected the whole study region; we often found pieces of charcoal in the cones, most often at depths of ca. 20 cm. Secondly, there is a mediaeval castle in the area; it was burnt in 1447. Anthropogenic remnants (ceramics) are occasionally found at depths of 15-35 cm. Obviously, both types of material may have been re-transported along the slopes, and thus any such record has to be interpreted with great caution. Nevertheless, both these sources of information indicate mean values of 10 cm of sand per 100 yr. However, the occurrence of layered sand/organic matter cones makes clear that these figures have to be interpreted as long-term average rates of processes that are inherently episodic.

Effects of mesoclimate

The effect of mesoclimate on cone vegetation seems to be generally small; a surprising result in view of rather strong mesoclimatic gradients across the canyons (Zittová-Kurková 1984). Potential direct solar irradiation in several spring months is weakly correlated with the floristic composition of cones while the position above the canyon bottom (this variable is strongly correlated with the likelihood of temperature inversions; Zittová-Kurková 1984) was essentially uncorrelated with the species composition. The importance of these factors is much lower than that of disturbance and cannot unequivocally be separated by statistical techniques.

The low impact of climate on species composition could in principle be due to two non-exclusive causes: (1) poor relationship between the position variables as defined in the current study and the major mesoclimatic gradients, and (2) a real weak effect of the mesoclimate on vegetation. The first explanation is not likely to be true since the altitudinal gradient is indeed the major source of mesoclimatic variation well captured by the position variables. For example, the temperature difference on a day in June between rock tops and canyon bottoms may reach 15 °C and the duration of snow cover may differ by six to eight weeks (Zittová-Kurková 1984; Gutzerová & Herben unpubl.). A further difficulty lies in the fact that the position variables are, to some extent, correlated with the structural variables, the effect of mesoclimate is indeed not independent of the disturbance gradient; cones positioned higher up the valley sides are on the average steeper (Table 3). Owing to this, the importance of the two sets of factors cannot be fully separated by statistical analyses.

Nevertheless, we conclude that the effect of climate on sandstone vegetation is indeed weak. The sandstone flora is extremely poor in species, with only a few species with specific ecological demands. The number of species whose distributions are determined by mesoclimate (*Plagiothecium undulatum, Sphagnum fimbriatum, Mnium hornum, Dryopteris* spp. occurring on the ‘cold’ cones; *Cetraria islandica,* *Sphagnum capillifolium, Lophozia ventricosa* occurring on the 'warm' cones) is clearly less than the number of species that respond to the disturbance gradient.

Peat accumulation

A specific type of cone development is brought about by the growth of *Sphagnum* and the accumulation of peat. *Sphagnum* peat accumulations were found to be 3-43 cm thick. On some cones they are buried by sand of 5-50 cm thickness (N. Gutzerová unpubl.). The occurrence of peat development at steep slopes indicates no recent history of rejuvenation by sand sedimentation. Nevertheless, much of the variation in the occurrence and development of peat accumulation in cones appears unpredictable. This may have several reasons. First, several *Sphagnum* species with different niches occur there (mainly *S. capillifolium*, *S. girgensohnii*, *S. quinquefarium* and *S. fimbriatum*). For example, *S. fimbriatum* is a species of wet cold canyon bottoms, whereas *S. capillifolium* occurs predominantly in drier and warmer positions. Second, the initiation of peat accumulation may be due to stochastic factors; once it begins, then it is essentially autocatalytic as the water retention of the peat enhances further *Sphagnum* growth (Malmer et al. 1994).

Sphagnum production on the cones is of the same magnitude as reported for terrestrial peat bog *Sphagnum* (for a review, see e.g. Lindholm & Vasander 1990). From the organic matter density in *Sphagnum* peat, we estimate the accumulation of a peat deposit the 40 cm thick to take ca. 400 yr in the absence of decomposition. Owing to the extreme slowness of *Sphagnum* decomposition, the estimates of *Sphagnum* decomposition add considerable uncertainty to the argumentation. It seems to be well established that after an initial decrease in mass further decrease is very slow (see also e.g. Rochefort et al. 1990). It remains unclear whether the initial shape of the decomposition curve can be confidently used for projection. The linear model (which yields time-to-full-decomposition to be 43 yr) is certainly incorrect, since it is likely to be affected by the faster mass decrease at the beginning of the decomposition, but even the exponential model may be unrealistic since its fit was lower than that of the linear model. *Sphagnum* systems litter bags are known to overestimate the rate of decomposition relative to indirect (long-term) methods (Belyea & Warner 1996). The matter is further complicated by the physical squeezing of the matter (Økland & Ohlson 1998) whose rate is unknown at sloping surfaces. Nevertheless, *Sphagnum* peat accumulation seems to be a process that occurs at essentially similar time scales as the long-term rate of sand sedimentation.

Conclusions

A disturbance-driven succession can be demonstrated for sandstone talus cones with a reasonable certainty. The change of species composition during this succession seems to be rather regular, with bryophytes and grasses dominating in the early stages and ericaceous shrubs in the later stages. Repeated episodes of sand deposition lead to frequent rejuvenation of the cones; if the sand deposition is limited, the rejuvenation is constrained to the upper part of a cone, leading to within-cone differentiation in the successional age. At a landscape level, these cones form a system of patches of different successional ages with a species composition differing according to the age of the particular patch and thus significantly contributing to the species richness of the area.

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