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Succession of Vegetation on Dumps from Strip Coal Mining, N. W. Bohemia, Czechoslovakia

Keywords

Primary succession, Higher plants, Dumps from brown coal mining, Species composition Species diversity, Ordination.

Abstract

Prach K. (1987): Succession of vegetation on dumps from strip coal mining, N.W. Bohemia Czechoslovakia. — Folia Geobot. Phytotax., Praha, 22: 339—354. — The primary succession of vegetation (higher plants) was studied on large dumps from brown coal mining in N.W. Bohemia, Czechoslovakia. Three differently aged stages were investigated (1977—1986), using permanent plots and transects. Changes in the species composition, the participation of life forms, and the species diversity were expressed on the basis of cover data for a period of 30 years of the succession. The data were processed by an ordination technique (DCA).

INTRODUCTION

Mining activities create new substrata open to colonization by organisms. In Central Europe, brown coal (lignite) mining, owing to its large-scale dimensions and the severity of the disturbances caused, has an important influence on the landscape. One of the most affected regions is the Most Basin in N. W. Bohemia, Czechoslovakia, spreading along the Krušné Hory Mts. (Erzgebirge). Brown coal is exploited mostly by open-cast mining in layers reaching now, in some cases, nearly 200 m in depth, with prognosis to 300 m. Naturally, such a huge amount of waste material must be deposited somewhere. In N. W. Bohemia there are now about 200 km² of dumps. In future, their area will cover c. 400 km². Some of this area is reclaimed but large dumps are left without any treatment after dumping. Thus a spontaneous succession can be followed there.

The dumps from brown coal mining were considered a very suitable object for the study of succession, especially because of their large dimensions, exact dating and relatively homogeneous substratum. The great heterogeneity of the relief, causing marked horizontal heterogeneity of the vegetation, is a major disadvantage. However, this heterogeneity on a micro- and meso-scale is regularly repeated over of hectares and square kilometres. Therefore these dumps seemed more suitable for the study of population processes than for community-level approaches which require more homogeneous material.

The succession of vegetation on dumps from brown coal mining has been studied frequently in North America (Bramble et Ashley 1955, Sindelar et Plantenberg 1978, Archibold 1980, Bell et Ungar 1981, etc.). In Czechoslovakia, several papers have appeared dealing with zoological problems (Bejček 1983, Bejček et Tyrner 1980, Hejkal 1985) as well as vegetation processes (Toběrná 1969, 1980, Volf et Pyšek 1986, Lukešová et Komárek 1987, Prach 1984, 1986 a 1987). This paper summarizes a 10-year study, integrating the author's papers mentioned above.

METHODS AND STUDY SITES

All dumps studied are located in the surroundings of the town of Most c. 80 km W.N.W. of Prague, at an altitude of 250 to 270 m. In the period from 1977 to 1982, the mean annual temperature was 8.5° and the average annual precipitation 470 mm (data from the meteorological station at Kopisty near Most, in the vicinity of the study plots). The dumps are formed mostly by grey clay from the Miocene period (88 % according to Jonáš 1972), with inserts of sand and gravels, occasionally of other substrata including soil horizons. Basic chemical properties of the grey clay (Štýs 1981): SiO_2 — 57 %, Al_2O_3 — 16 %, Fe_2O_3 — 4 %; MnO — 0.12 %; MgO — 1.64 %; CaO — 0.6 %; Na_2O — 0.25 %; K_2O — 2.47 %; P_2O_5 — 0.44 %; SO_3 — 0.25 %; total N — 0.12 %.

For the long-term study of succession, a complex of variously aged younger dumps (0 to 12 years at the beginning of the study) and the oldest (24 years) large dump in the region were chosen. The former dumps are located in the centre of the industrial area between the towns of Most and Litvínov, the latter, the oldest, lies on the margin of the area, at the foot of the Krušné hory Mts., c. 6 km to SSW from the other dumps (Fig. 1).

Four dumps were studied in detail by means of permanent plots and random and permanent transects. Micro-mapping (Knapp 1974) in the plots of 5×5 m and a point-quadrat technique were used for data collection. A point-quadrat apparatus with a moving needle was constructed by M. Rejmánek, inspired by similar devices (Kershaw 1973, etc.). The needle was dropped down at regular intervals of 10 cm (on permanent plots of 1 m² and on transects 50 m long) and of 20 cm (along 100 m transects). Presence/absence data were registered giving estimates of cover degrees (total, and of particular species).

The stages studied:

Stage A: Three permanent plots 5×5 m were drawn up on pure clay in the first year of the existence of the dump in 1977 and folowed by vegetational mapping till 1986.

Stage B: Four plots 5×5 m were also marked in the first year of the existence of this dump (1979) and followed by "micromaps" until the partial destruction of the dump in the autumn of 1983; random transects of 100 m were drawn during this stage in 1982 and 1984 (on the part left untouched); in 1985, all this stage was destroyed; clay mixed with sand and gravels formed the dump.

Stage C: It was studied from the 12th year of its existence in 1979 till 1986; the point-quadrat method was used in 10 permanent quadrats of 1 m², fixed randomly along a transect of 30 m; in the autumn of 1983, the plots were destroyed and, in 1985, a permanent transect was fixed in an adjoining untouched part of the dump; in 1982, a random transect of 100 m was elaborated; clay was a predominant substratum here.

Stage D: This stage was studied from the 24th year in 1979 till 1986, i.e. till the 31st year of the existence of the dump; 10 quadrats of 1 m² were elaborated by the same manner as at Stage C; one random transect of 100 m was made in 1982; the dump is formed mostly by clay, sand and gravels are only sporadic.

Some other stages were studied, too, but they existed only for a short time, owing to disturbance by mining and post-mining activities. Nevertheless, they provided us with other valuable information, which made some comparison and generalization possible.

It was necessary to use different methods for the vegetation analysis of the particular stages because of great differences in the character of the vegetation cover. At the youngest stages, where the vegetation cover was only sporadic and particular specimens were large, it was not possible to use small permanent plots; using permanent transects was not convenient because repeated exact localization in subsequent years would have been difficult. The use of "micromaps" seemed to be the best solution. On the other hand, for the older successional stages with a closed vegetation, micro-scale mapping would not have been reliable. A combination of transects and small permanent quadrats, elaborated by the point-quadrat technique, seemed to be the most suitable. Data obtained by the same method in the individual stages in particular years were averaged and are surveyed in Table 1. Evidently, cover degrees obtained by means of micro-scale mapping are over-estimated compared with those of the point-quadrat. The analyses of vegetation were made in the middle of September, at the time when most of the vegetation was best developed.

According to the cover data obtained by the described methods and extensive observations, phytosociological relevés and experience from other plots and dumps, schemes of dominant species changes, and the participation of life forms during the first 30 years of the succession were constructed.

Species diversity was calculated by Shannon's formula (Whittaker 1972) from the cover data of Table 1. Binary logarithms were used.

The cover data were further processed by the DCA ordination technique (Detrended Correspondence Analysis — Hill 1979). Both samples and species were ordinated. A matrix of 34 samples and 31 species was used. Only those species which participated with a cover degree higher than 2 % in at least one sample were taken into consideration. The cover data were transformed to an ordinal scale from 0 to 7 (corresponding values: 1 = cover of 0.1 %; 2 = 1.0 %; 3 = 5.0 %; 4 = 25.0 %; 5 = 50.0 %; 6 = 75.0 %; 7 = 100 %) close to the span given by the 7-degree Braun-Blanquet scale.

The nomenclature is according Neuhäuslová et Kolbek (1982).

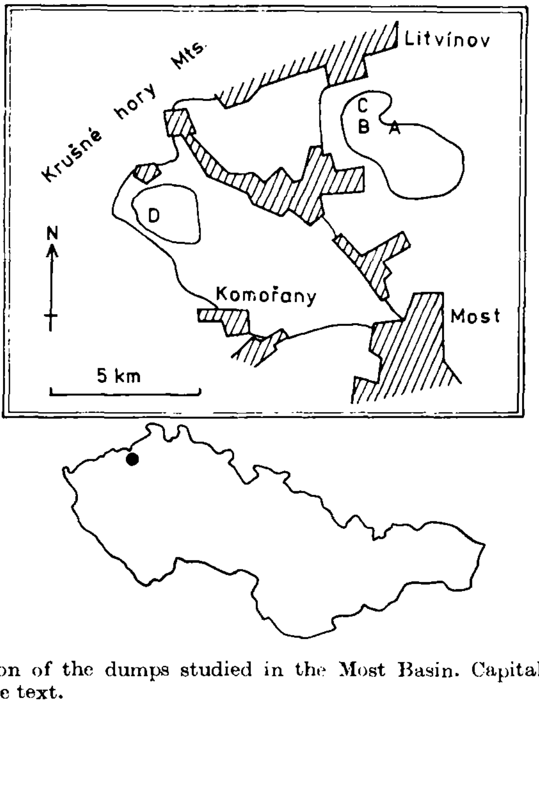

Fig. 1. The localization of the dumps studied in the Most Basin. Capitals correspond to the stages described in the text.

RESULTS

1. General description of the succession

The succession on the dumps shows several distinct features of a primary succession: it starts on undeveloped soil, on substrata not previously colonized by organisms, with a nearly zero primary seed bank. Only the upper soil layers, exceptionally stripped and dumped, can contain some viable diaspores, locally important for further development of the vegetation. A small amount of diaspores can also contaminate a substratum during transport to the dumps. But at the moment when the succession starts, the total number of diaspores is negligible in the scale of a whole dump. Thus, transport of diaspores from the surroundings of a dump is decisive for the subsequent development of the vegetation.

Besides the transport of diaspores by wind, zoochory is also important, especially in the initial stages, when the survival and germination of light anemochorous seeds are less probable than those of zoochorous seeds which are mostly larger (HAYASHI 1979). The mean annual input of seeds from the surrounding landscape was estimated only at several tens of seeds per 1 m^2 (assessed by a soil sample analysis of the 1-year old stage, using a method adapted from KROPÁČ 1966).

The successful establishment of species further depends on successful germination and on a pre-reproductive mortality. Both characteristics are strongly determined by the variability of abiotic factors, especially moisture, throughout a dump. The variability is closely related to the heterogeneity of the relief and is influenced by the course of the weather in particular years, obviously as regards moisture and soil temperature.

Generally, depressions are much more convenient for the establishment of vegetation than are the tops of small hills and crests. This is supported by the fact that diaspores accumulate in the depressions through water transport and gravitation forces. (In the third year of the succession, the span of the diaspore number ranged from several tens on the tops to more than 60 000 per m^2 in the depressions — see PRACH 1987 for details.) Intensive intra- and later also inter-specific competition occurs in places densely covered with vegetation, while the dry tops are often bare (this is striking especially in about the 8th year of the succession). Overcrowding in populations is sometimes very high, accompanied by strong thinning effects (maximum seedling density was found to be 6 352 per 0.01 m^2 in one population of *Atriplex hastata*). However, abiotic factors seem to have a greater influence on pre-reproductive mortality in the initial stages than competition.

Very important for the subsequent development of the vegetation during the initial stages in particular years is the weather in the 2nd half of May and in June, when most annual species are at the stage of susceptible seedlings. If this period is dry and warm, the participation (cover degrees) of species like *Senecio viscosus, Polygonum lapathifolium, Chenopodium* spec. div., *Atriplex* spec. div., etc., can be markedly changed in the year concerned, and through the amount of diaspores produced, the vegetation can be influenced even in subsequent years. Despite extreme conditions in the initial stages on the dumps, most species can grow there if their diaspores find microsite conditions suitable for germination and further development. (Some diaspores can evidently survive for several years, until site conditions improve, and then germinate.)

Most perennial species of later successional stages are already present in the first three or four years of the succession but only with a very low cover degree, on the most suitable sites. Some of them grow into large, luxuriant forms where they have no competition. The limitation of the establishment of later successional perennial species probably operates at the levels of germination and/or seedling development. In these phases of their life cycle, the perennials seem to be more susceptible than the annuals. On the other hand, surviving, established specimens of perennials were more resistant in a dry period because their larger root systems can reach deeper and wetter layers of the substratum than those of most of the annuals. (At a depth of c. 30 cm, there is a zone where water condenses, making the layer permanently wet.)

The annuals and biennials, predominating in the first years of the succession, are gradually replaced by perennials, up to the 15th year (see Fig. 2b). Simultaneously, interspecific competition and probably allelopathy start to play a decisive role in community development and organization. The annuals (*Atriplex nitens, Sisymbrium loeselii*, etc.) and biennials (*Carduus acanthoides*) are gradually shifted to less suitable

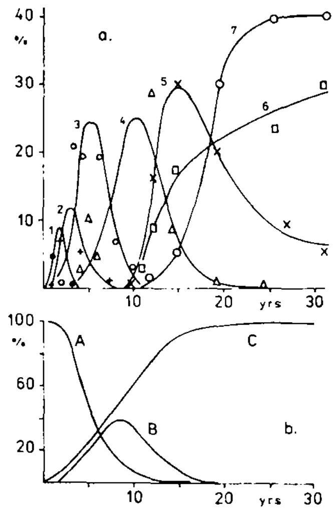

Fig. 2

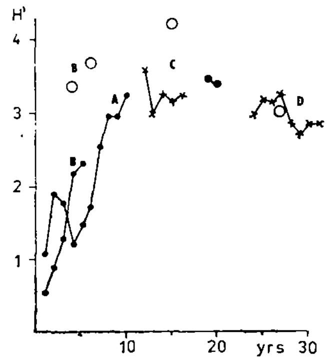

Fig. 3

Fig. 2. (a) Changes of the dominant species during 30 years of the succession on the dump expressed in cover percentages; 1 (full points) — *Polygonum lapathifolium*; 2 (crosses) — *Senecio viscosus*; 3 (small open circles) — *Atriplex nitens*; 4 (triangles) — *Carduus acanthoides*; 5 (x) — *Tanacetum vulgare*; 6 (squares) — *Calamagrostis epigejos*; 7 (larger open circles) — *Arrhenatherum elatius*; the symbols represent the averaged values of Table 1.
(b) Dominance of the life forms on the base of cover degrees: annuals (A), biennials (B), and perennials (C).

Fig. 3. Changes in species diversity H', based on cover degrees. The same plots and transects are connected by full lines. Explanations of the symbols: Small dots — the permanent plots 5×5 m on Stages A and B, followed by the micro-scale mapping; Crosses — the permanent plots 1×1 m for the point-quadrat on Stages C and D; Open circles — the 100 m random transects on Stages B, C, and D; Larger dots — the 50 m permanent transect on Stage C.

Table 1. Participation of particular species in the succession (average cover percentages; species with 2 % of cover and more at least in one average sample, are listed). Data obtained by micro-scale mapping (M), by point-quadrat technique in permanent plots (P) and along transects (PT)

Stage	A										B						
Age	1	2	3	4	5	6	7	8	9	10	1	2	3	4	4	5	6
Year	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1979	1980	1981	1982	1982	1983	1984
Method	M	M	M	M	M	M	M	M	M	M	M	M	M	M	PT	M	PT
1. *Polygonum lapathifolium*	8.9	16.9	0.2	+	+	0.7	0.5	0.3	+	0.2	.	0.3	+	.	.	.	.
2. *Polygonum arenastrum*	2.1	1.5	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.
3. *Chenopodium polyspermum*	+	3.9	+	+	+	+	.	.	+	.	.	.	.	.	.	.	.
4. *Matricaria maritima*	+	0.8	0.3	+	0.3	0.7	2.0	8.1	0.9	.	.	.	.	.	2.4	+	1.4
5. *Senecio viscosus*	.	1.1	0.8	13.3	0.2	1.1	3.2	1.6	0.4	0.4	+	14.6	.	+	0.9	3.3	5.0
6. *Atriplex nitens*	0.6	0.3	5.8	0.3	1.9	32.5	20.2	6.6	4.6	2.8	1.3	1.1	39.1	24.1	38.8	9.8	7.0
7. *Cardaria draba*	+	2.7	9.4	18.4	18.6	10.3	7.3	6.2	6.4	7.1	.	.	.	.	0.2	.	.
8. *Sisymbrium loeselii*	.	.	.	.	+	1.8	+	4.4	13.7	3.9	.	+	1.8	13.5	5.3	1.4	9.0
9. *Carduus acanthoides*	+	+	1.9	0.7	13.4	1.6	3.7	3.8	3.4	0.7	.	+	2.6	3.2	3.5	1.6	5.0
10. *Artemisia vulgaris*	.	.	+	+	+	2.2	6.1	18.8	21.2	17.7	.	.	.	.	1.6	+	6.0
11. *Chamerion angustifolium*	.	.	.	.	.	.	.	+	0.5	1.1	.	+	+	2.6	2.9	2.8	9.6
12. *Cirsium arvense*	.	.	.	.	+	+	0.8	1.1	1.9	2.3	+	+	0.3	1.2	5.6	1.5	3.8
13. *Rubus idaeus*	.	.	.	.	.	.	.	.	.	.	+	+	5.5	12.1	2.9	17.4	9.4
14. *Rubus fruticosus agg.*	.	.	.	.	0.2	+	0.2	.	+	+	.	.	.	.	3.4	.	0.4
15. *Holcus lanatus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2.1	+	0.2
16. *Tussilago farfara*	.	.	.	.	.	.	.	+	0.4	0.5	.	.	+	.	4.5	+	6.2
17. *Calamagrostis epigejos*	.	.	.	.	.	.	.	+	0.4	3.8	.	.	.	.	0.4	.	.
18. *Tanacetum vulgare*	.	.	.	.	.	.	.	.	0.3	1.2	.	.	.	.	0.4	.	0.4
19. *Lathyrus tuberosus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
20. *Poa palustris* subsp. *xerotica*	.	.	.	.	.	.	.	.	0.2	0.7	.	.	.	.	.	.	.
21. *Elytrigia repens*	.	.	.	.	.	.	.	+	0.4	0.6	.	.	.	.	.	.	.
22. *Rumex acetosa*	.	.	.	.	.	.	+	.	.	.	.	.	.	.	0.3	0.5	.
23. *Convolvulus arvensis*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
24. *Potentilla reptans*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
25. *Hypericum perforatum*	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
26. *Linaria vulgaris*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
27. *Senecio fuchsii*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
28. *Hieracium sabaudum*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
29. *Achillea millefolium*	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
30. *Arrhenatherum elatius*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
31. *Deschampsia cespitosa*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 1 (cont.)

Stage	C								D								
Age	12	13	14	15	15	16	18	19	24	25	26	27	27	28	29	30	31
Year	1979	1980	1981	1982	1982	1983	1985	1986	1979	1980	1981	1982	1982	1983	1984	1985	1986
Method	P	P	P	P	PT	P	PT	PT	P	P	P	P	PT	P	P	P	P
1. *Polygonum lapathifolium*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2. *Polygonum arenastrum*	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
3. *Chenopodium polyspermum*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
4. *Matricaria maritima*	0.7	.	0.4	.	0.4	.	.	.	.	.	.	.	.	.	.	+	0.2
5. *Senecio viscosus*	.	.	0.4	2.5	.	.	.	.	.	.	.	.	.	.	.	.	.
6. *Atriplex nitens*	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
7. *Cardaria draba*	7.6	5.4	3.9	3.6	9.3	3.2	1.2	0.2	.	.	.	.	0.2	.	.	.	.
8. *Sisymbrium loeselii*	5.9	0.6	0.3	5.4	3.5	0.2	.	.	.	.	.	.	.	.	.	.	.
9. *Carduus acanthoides*	31.2	7.3	9.8	2.7	3.0	.	0.2	.	0.4	+	+	0.3	0.2	.	.	.	.
10. *Artemisia vulgaris*	0.4	.	0.3	+	0.2	2.1	.	0.2	0.4	0.4	0.2	.	0.2	.	.	.	.
11. *Chamerion angustifolium*	2.7	2.5	2.8	3.1	3.5	0.2	.	0.2	0.4	0.6	0.2	0.2	.	.	.	.	0.3
12. *Cirsium arvense*	5.7	12.8	14.7	14.7	21.1	11.3	5.2	6.2	1.7	2.5	3.7	3.7	7.3	4.0	3.4	4.1	4.7
13. *Rubus idaeus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
14. *Rubus fruticosus agg.*	0.3	.	0.5	0.8	9.1	1.5	17.6	16.0	3.0	4.7	5.8	5.7	0.3	8.5	6.9	4.2	5.6
15. *Holcus lanatus*	9.3	38.6	37.6	26.4	6.5	27.5	12.0	8.4	.	.	.	.	.	.	.	.	.
16. *Tussilago farfara*	6.4	16.7	17.2	11.0	1.9	3.3	0.2	.	32.5	31.4	22.8	21.6	31.9	12.4	2.9	5.5	5.1
17. *Calamagrostis epigejos*	9.3	10.4	11.1	11.1	23.3	20.3	39.4	41.4	19.4	23.7	22.1	27.0	22.9	28.9	29.5	32.9	30.7
18. *Tanacetum vulgare*	16.8	32.1	29.2	50.8	9.7	44.0	17.6	20.0	12.3	14.5	10.0	14.7	6.3	16.0	5.0	6.9	7.3
19. *Lathyrus tuberosus*	3.8	15.8	11.6	13.1	6.7	10.6	5.0	2.4	3.5	6.9	4.7	3.3	0.9	2.6	1.6	1.3	2.9
20. *Poa palustris* subsp. *xerotica*	0.2	.	0.6	1.9	10.8	5.5	3.6	4.6	3.7	5.6	4.1	6.7	10.1	6.2	5.5	4.6	2.1
21. *Elytrigia repens*	10.0	14.5	0.5	4.1	25.0	6.4	4.6	2.0	.	.	0.6	1.3	1.8	.	.	0.5	.
22. *Rumex acetosa*	.	.	2.1	3.1	5.5	4.6	3.2	5.2	.	.	.	.	.	.	.	.	.
23. *Convolvulus arvensis*	0.8	.	.	0.3	10.1	.	19.6	19.2	3.2	3.3	3.1	6.3	18.4	6.6	1.9	4.1	7.7
24. *Potentilla reptans*	.	.	.	.	3.6	.	.	.	.	.	.	.	0.9	.	.	.	0.2
25. *Hypericum perforatum*	2.2	.	0.2	.	.	.	1.2	0.6	.	.	.	.	1.4	.	.	.	+
26. *Linaria vulgaris*	2.6	.	0.2	+	0.9	.	3.2	4.6	0.9	2.3	0.3	0.2	0.1	0.3	.	+	+
27. *Senecio fuchsii*	.	.	.	.	2.0	.	0.8	.	.	.	.	.	0.3	.	.	.	.
28. *Hieracium sabaudum*	.	.	.	.	+	.	0.2	.	1.6	1.2	1.1	2.6	0.6	1.6	0.3	0.7	0.7
29. *Achillea millefolium*	.	.	.	.	0.2	.	.	.	8.9	10.2	8.8	8.4	1.0	7.8	3.0	3.3	3.6
30. *Arrhenatherum elatius*	1.7	2.3	1.3	3.1	5.8	11.4	31.6	29.0	41.4	43.9	40.9	31.9	49.5	37.4	40.6	46.9	45.5
31. *Deschampsia cespitosa*	.	.	.	.	.	.	0.2	.	0.6	1.8	2.2	2.6	.	3.0	3.8	3.5	1.9

\+ – Cover of 0.1 % and less

sites, mostly the tops, of the dumps away from the strong competition of robust perennial plants (*Cirsium arvense, Tanacetum vulgare, Calamagrostis epigejos*, etc.). Generally, the succession seems to run more slowly at such sites than at more suitable ones. Thus we can speak of an "asynchronous succession". Species typical of the early successional stages can re-occur later only at sites occasionally disturbed by animals (*Sus scrofa, Microtus arvalis*, etc.) or exceptionally by other factors, e.g. soil slide. All these disturbances are usually small-scale.

By the 15th year of the succession, the vegetation reaches a close character with nearly 100 % of cover. During further development, grasses gradually expand, represented largely by a ruderal species, *Calamagrostis epigejos* and a typical species of mesic grassland, *Arrhenatherum elatius*. The latter is still the dominant species on the oldest dump observed (31 years old at the present time), forming a rather stabilized population without any evident directional changes in its cover and vitality. *Calamagrostis epigejos* slowly expanded during this stage, conquering forbs like *Tanacetum vulgare* and *Tussilago farfara*.

Spontaneous establishment of woody species is limited by unfavourable abiotic conditions in the initial stages, and by strong competition from the herb layer in the later stages, resulting in only about 10 % of cover about the 15th year and lasting till about the 30th year of the succession without apparent changes. *Sambucus nigra* is the only plant which can commonly grow on the dumps immediately after their creation, with the optimal population development between the 15th and 20th years of the succession. In the 30th year, some specimens of *Sambucus nigra* were already dead or nearly dead. Several other woody species were noted at later successional stages: *Betula pendula, Fraxinus excelsior, Acer pseudoplatanus, Salix caprea*, occasionally others, but only scattered and not spreading apparently.

In the succession described, we can distinguish the following large-scale stages (the scheme is simplified, one stage changes to the next gradually, with a great temporal-spatial pattern; some other stages can develop on a small-scale under specific conditions):

1. An initial stage with various annuals (mostly *Polygonum lapathifolium* and *Senecio viscosus*), reaching a low total cover; it generally lasts from the lst to the 3rd year of the succession.
2. A stage dominated by *Atriplex nitens*, generally from the 4th to the 6th year; many other species are present but with a low cover degree.
3. A stage with biennial *Carduus acanthoides* and winter annual *Sisymbrium loeselii* in about the 7th to the 12th year; this stage is sometimes less evident.
4. A stage with robust perennial forbs, mainly with *Tanacetum vulgare* and with scattered *Sambucus nigra;* the height of development is in about the 15th year of the succession.
5. A stage with grasses (*Arrhenatherum elatius, Calamagrostis epigejos*) and scattered *Sambucus nigra* and other woody species.

No definite conclusions regarding later successional development can be made because we do not know any older representative stage than that of 30 years. However, we can assume that the stage with dominant *Arrhenatherum elatius* and *Calamagrostis epigejos* will probably last for a long time. It may be considered an arrested successional stage or "subclimax" (WHITTAKER 1974). It can also be seen as a terminal "ruderal steppe-forest community".

The general successional trends described here are illustrated by Table 1 and Fig. 2, where changes of dominant species and the participation of annuals, biennials, and perennials are given. The sequence of the dominant species is generalized and averaged for large dumps in the region involving a large-scale mosaic. This order can differ from site to site. Other species can dominate locally, e.g., *Sisymbrium loeselii*, *Cardaria draba*, *Holcus lanatus*, *Tussilago farfara*, *Chamerion angustifolium*, *Elytrigia repens*, as mentioned above, depending on the relief and other environmental factors. Randomness and the vegetation history of a site are also important. On inserts of gravels, sand, soil horizons, etc., the succession runs generally at a higher rate and with a higher species number in the first years, later the differences in the substratum are not so evident. Some species invade dumps predominantly from their banks and margins, e.g. *Arrhenatherum elatius*. Very exceptional inserts of toxic substrata arrest the succession for a long time. All these phenomena cause a further increase in the spatial-temporal heterogeneity of the vegetation. Despite these facts, the results seem to reflect well the general course of the succes sion

2. Changes in species number and diversity

It is rather surprising that most species participating in the succession were noted as early as in the first few years of the succession, naturally with a very low cover degree. The highest species number was found in the 5-year-old dump (for details see PRACH 1986a). Later, the species number declines under strong competition from robust forbs and grasses.

The course of species diversity generally shows similar features, with the maximum between the 12th and 15th years of the succession. It is somewhat later than the maximum of species number: about the 5th year, there is one dominant species present (*Atriplex nitens*) and many other species occur sporadically in an unclosed cover of vegetation. Later, the species with less competitive ability are mostly excluded but no strong dominant species occurs between the 12th and 15th years. Species evenness is the highest at this time. The most common species, *Tanacetum vulgare*, *Calamagrostis epigejos*, *Chamerion angustifolium*, *Carduus acanthoides*, *Holcus lanatus*, *Elytrigia repens*, etc., form a distinct patch structure until *Tanacetum*, temporarily, and competitive grasses (*Calamagrostis epigejos* and *Arrhenatherum elatius*) prevail. This is the time of the culmination of species diversity (Fig. 3).

The different sampling methods have provided rather different values of species diversity (Fig. 3). It is clear that the 100 m transects reflected vegetational heterogeneity in a meso-scale view best, resulting in the highest figure of H′. That is especially the case of the middle-aged dump (see above). In the oldest dump, the vegetation cover is more uniform in the meso-scale view, therefore there are no differences apparent between values obtained from the transect and the 1 m^2 plots.

At the beginning of the succession, species diversity fluctuations can be large, caused by strong temporal prevalence of one species in some years. Later, only small fluctuations were detected. (In the year of the large fluctuation shown in Fig. 3, there was a wet period at the beginning of summer, which supported strong dominance by *Senecio viscosus* — see Table 1 and Fig. 6).

3. Results of the ordination procedure

Data of Table 1 were processed by the DCA technique: The samples were arranged very clearly according to their successional age which is reflected at the X-axis (Fig. 4). The position of the last year's sample of Stage A is near that of the first year of the observation of Stage C, i.e. at 10 and 12 years of age, respectively. The convergence of both the early stages to Stage C is evident. Differences between initial positions of Stages A and B are caused especially by the participation of expanding *Rubus idaeus* in Stage B and its absence in Stage A. The rate of succession can be seen to decrease in the results. The slight back-shift of the last two samples of Stage D probably reflects a rejuvenation of some permanent quadrats caused by *Sus scrofa* burrowing after which species like *Matricaria maritima* appeared, regenerating from dormant seeds (see Table 1).

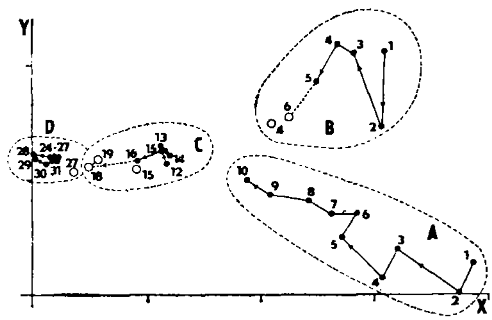

Fig. 4. Ordination (DCA) of the samples from Table 1. Figures mean the age of the stages. Small dots represent the stages followed by the permanent plots, larger dots those by the transects. The same stages are connected by full lines if the same permanent plots or transects were used, or by dotted lines if the sampling methods were changed. The capitals refer to Stages A, B, C, and D.

The ordination of the species (Fig. 5) also reflects their successional status clearly, arranging them along the X-axis from the annuals on the right side of the ordination diagram, through robust forbs prevailing in the middle part, to late successional grasses and forbs on the left side of the diagram. The sequence of the dominant species corresponds well with that in Fig. 2a.

DISCUSSION

In the succession on the dumps, processes described by all three models of succession proposed by Connell et Slatyer (1977) can be recognized. Despite the generally extreme abiotic environmental factors, *tolerance* model processes seem to prevail there. All the dominant species characteristic of the later successional stages were present in the first five years of the succession at least in several specimens. But the classical Clementsian view of succession, represented by the *facilitation* model of Connell and Slatyer, can also be applicable, especially to vegetation changes on more extreme sites. It was often noted that some perennials, e.g., *Calamagrostis epigeios, Tanacetum vulgare, Elytrigia repens,* became established more readily in a cover of annuals or biennials, e.g., *Atriplex nitens, Carduus acanthoides.* The *inhibition* model processes were apparent in limited places which were occupied by species forming a compact cover, established mostly by vegetative spreading (*Cardaria draba, Calamagrostis epigejos*).

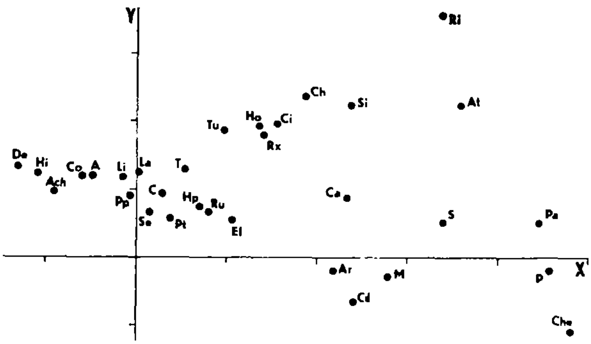

Fig. 5. Ordination (DCA) of the species.
Abbreviations (from right to left): Che — *Chenopodium polyspermum*, P — *Polygonum lapathifolium*, Pa — *Polygonum arenastrum*, S — *Senecio viscosus*, At — *Atriplex nitens*, Ri — *Rubus idaeus*, M — *Matricaria maritima*, Si — *Sisymbrium loeselii*, Ca — *Carduus acanthoides*, Cd — *Cardaria draba*, Ar — *Artemisia vulgaris*, Ch — *Chamerion angustifolium*, Ci — *Cirsium arvense*, Rx — *Rumex acetosa*, Ho — *Holcus lanatus*, Tu — *Tussilago farfara*, El — *Elytrigia repens*, Ru — *Rubus fruticosus* agg., Hp — *Hypericum perforatum*, T — *Tanacetum vulgare*, Pt — *Potentilla reptans*, C — *Calamagrostis epigejos*, Se — *Senecio fuchsii*, La — *Lathyrus tuberosus*, Pp — *Poa palustris xerotica*, Li — *Linaria vulgaris*, A — *Arrhenatherum elatius*, Co — *Convolvulus arvensis*, Ach — *Achillea millefolium*, Hi — *Hieracium sabaudum*, De — *Deschampsia cespitosa*.

Generally, the models seem to be more applicable to relations between concrete populations than to the whole course of a succession. This depends largely on realized competitive relations between populations under given conditions. For example, when the density and vitality of a settled population are high, this population can inhibit the establishment of potentially invading successive populations and the *inhibition* model can be applicable. If the density and vitality of a population of the same species are low, the *tolerance* or the *facilitation* models can be considered. In a succession, heterogeneous in space and time, such as that on the dumps, the resulting situation can differ from site to site and can change in the course of time. It was even observed that inside one polycormon, e.g. of *Cardaria draba*, the establishment of later successional species was inhibited in patches with a higher density of the former species and facilitated elsewhere. It also could be seen that establishment was inhibited in a particular part of the polycormon in one year, and facilitated in a subsequent year in the same place, depending largely again on the density of the former species. It is evident that the scale of our view in space and time is decisive for our conclusions in this respect.

At about 15 years in the succession the most important community characteristics exhibited marked changes in their course. Species diversity, the aboveground

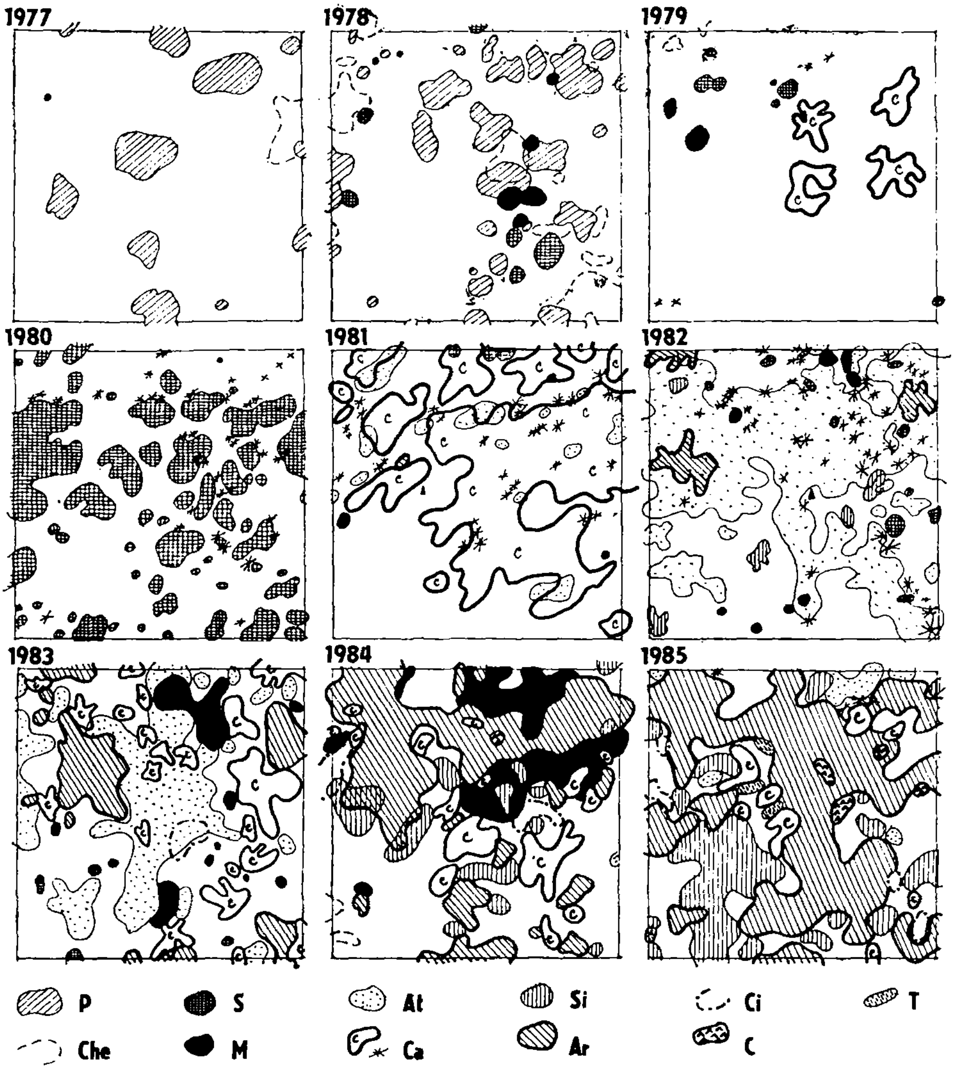

Fig. 6. An example of vegetation changes in one permanent plot 5 × 5 m on Stage A during the first nine years of the succession. The same abbreviations are used as in Fig. 5.

biomass of the herb layer, seed production, and the seed bank (PRACH 1983) reached their maximum. By the same time, the vegetational cover was getting close, reaching nearly 100 %. Generally, it is possible to say that after 15 years, the main ecological characteristics of the primary succession on the dumps are roughly comparable with those in the first years of secondary succession, e.g. on abandoned fields in the same climatic region.

No large and repeated fluctuations in species diversity were evident, except in the very initial stages, as seems to be common in the case of secondary succession, especially in highly productive environments (cf. PEET 1978). The reason is that in the first stages with open vegetation cover, there is not strong competition among short-lived species and later, when perennial species with similar life forms prevail, the changes in their cover are gradual and relatively small. This seems to be typical of succession under unproductive conditions where the competitive abilities of potentially strong dominants are diminished (cf. PEET 1978, GRIME 1979, HUSTON 1979). This is in accordance with a general model of productivity and diversity changes during succession, proposed and discussed in another paper (PRACH 1986 b).

The abrupt changes in species diversity in the initial stage on some of the permanent plots, were mostly not the result of successional changes in the whole community but of fluctuations in weather conditions in the particular year, eliminating many and/or supporting one of the species. It reflects low constancy during the youngest stages (REJMÁNEK 1979). Later successional stages were very resistant to weather fluctuations. Dry periods in 1982 and 1983 did not cause any more evident changes in species participation (see Table 1).

Changes of higher plant species diversity exhibit nearly the same tendencies as those of small mammals (BEJČEK 1983) and of *Carabidae* species (HEJKAL 1985) on the same dumps. The species diversity of birds (BEJČEK et TYRNER 1980) increases rapidly at the beginning of the succession, later only slowly, especially with gradual vertical diversification of the vegetation cover. The number of species of soil algae culminates in the oldest stage (see LUKEŠOVÁ et KOMÁREK, this issue). Generally, species diversity changes show similar tendencies in most groups of the organisms studied. The changes in species number of vascular plants are very similar to those given by TOBĚRNÁ (1980).

Grime's concept of strategies (GRIME 1979) can be well applied to succession on the dumps. The principal species of the initial stages can be marked as R (*Atriplex nitens, Senecio viscosus, Polygonum lapathifolium*) or S-R (*Polygonum arenastrum, Chenopodium strictum*) strategists. Later, C-R strategists prevail (*Calamagrostis epigejos, Tanacetum vulgare, Elytrigia repens*). *Arrhenatherum elatius*, the dominant species of the late stages, should be considered more C strategist than other species but it exhibits some features of R strategy as well. It must be emphasized that Grime's strategies are not strict categories, in which particular species can be rigidly classified. The categories are relative, they must be considered largely in a relation to a set of species studied under a given span of ecological conditions (cf. GADGILL et SOLBRIG 1972). Rather than categories, they may be only tendencies in a constitution of species.

The categories of life forms (annuals, biennials, perennials) change characteristically as is common in most other successional series (MACMAHON 1980, etc.). The decreasing rate of succession was also expected (BORNKAMM 1981).

The results of ordination confirmed the suitability of the DCA technique for the elaboration of such a set of rather heterogeneous data in order to express successional trends (GAUCH 1982).

It is surprising that despite some deficiency of the main nutrients in the substratum, the rate of succession is comparatively high and specimens can develop into normal, sometimes even into luxuriant forms. Studies of changes in the chemical properties of the substratum have not yet revealed any marked increase in the nutrient content during the period of 15 or 20 years of the succession (cf. TOBĚRNÁ 1973, ŠTÝS 1981). Nitrogen fixation cannot be expected to play a significant role because of the low quantity of blue-green algae (LUKEŠOVÁ et KOMÁREK 1987) and, presumably, of other N-fixing microorganisms as well. These questions still remain open, their solution would require detailed studies.

The primary succession on the dumps in N.W. Bohemia runs comparably quicker than on dumps in drier regions (SINDELAR et PLANTENBERG 1978) or on toxic substrata including low pH (BELL et UNGAR 1981, etc.). But it runs more slowly than on most other disturbed sites in comparable regions (cf. PYŠEK 1977; KIESEL et al. 1985, etc.). Large dimensions result in a lesser and selective input of diaspores from the surrounding landscape, and the adversity of abiotic factors, especially low water supply, further inhibits the fast establishment of plants. Moisture conditions and sources of diaspores were also found to be decisive factors in a succession on dumps studied by SINDELAR et PLANTENBERG (1978). ARCHIBOLD (1980) emphasized the role of abiotic factors preventing the successful establishment of vegetation. He stated a figure of 2 387 seeds per square metre and a year trapped on new dumps, which is much more than in our case.

A successional scheme of plant communities, proposed for the same dumps by TOBĚRNÁ (1980), is simplified and rather unrealistic, due to failure to describe vegetation changes on the dumps by means of Zürich-Montpellier phytosociological units. The species composition described in this paper, is generally comparable with that given by VOLF et PYŠEK (1986) for several other dumps in the Most Basin.

The 10 years'study has made it evident that a population-ecological and autecological approach (population-level approach) is necessary for better understanding of succession on the dumps (cf. PEET et CHRISTENSEN 1980). The timing and measure of the particular phases of life cycles determine the dynamics of populations and by means of these the dynamics of whole communities, including their successional changes. The operating of ecological factors, both abiotic and biotic, can be viewed through their influence on the particular phases of life cycles of species participating in the succession. One can mention, for example, the high seedling mortality and low germination under dry conditions, the distribution of diaspores influenced by the relief, the damage of seeds by insects, the transport of diaspores by wind or animals, in the case of the dumps studied here. This population-level approach should be accompanied by a long-term study in permanent plots (cf. AUSTIN 1981).

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SUMMARY

Thirty years of the primary succession on dumps from brown coal mining, N. W. Bohemia, Czechoslovakia, can be characterized by the following tendencies:

The total cover of vegetation rises from zero to nearly 100 % in about the 15th year of the succession and later. Annuals prevail in the first five years, biennials show a maximum in about the 8th year and perennials dominate after 10 years of

the succession. The sequence of the main dominant species: *Polygonum lapathifolium, Senecio viscosus, Atriplex nitens, Carduus acanthoides, Tanacetum vulgare, Calamagrostis epigejos* and *Arrhenatherum elatius*. They form rather distinct community types, covering large areas. Woody species are sporadic, reaching up to c. 10 % of the cover only, after the 15th year of the succession. The establishment of woody species is limited by adverse abiotic factors at the beginning of the succession and by competition from the herb layer after 10 years of the succession. The highest species number was noted in the 5th year of the succession; species diversity reaches its maximum between the 10th and 15th years. The results of the ordination (DCA) well reflect the general successional trends.

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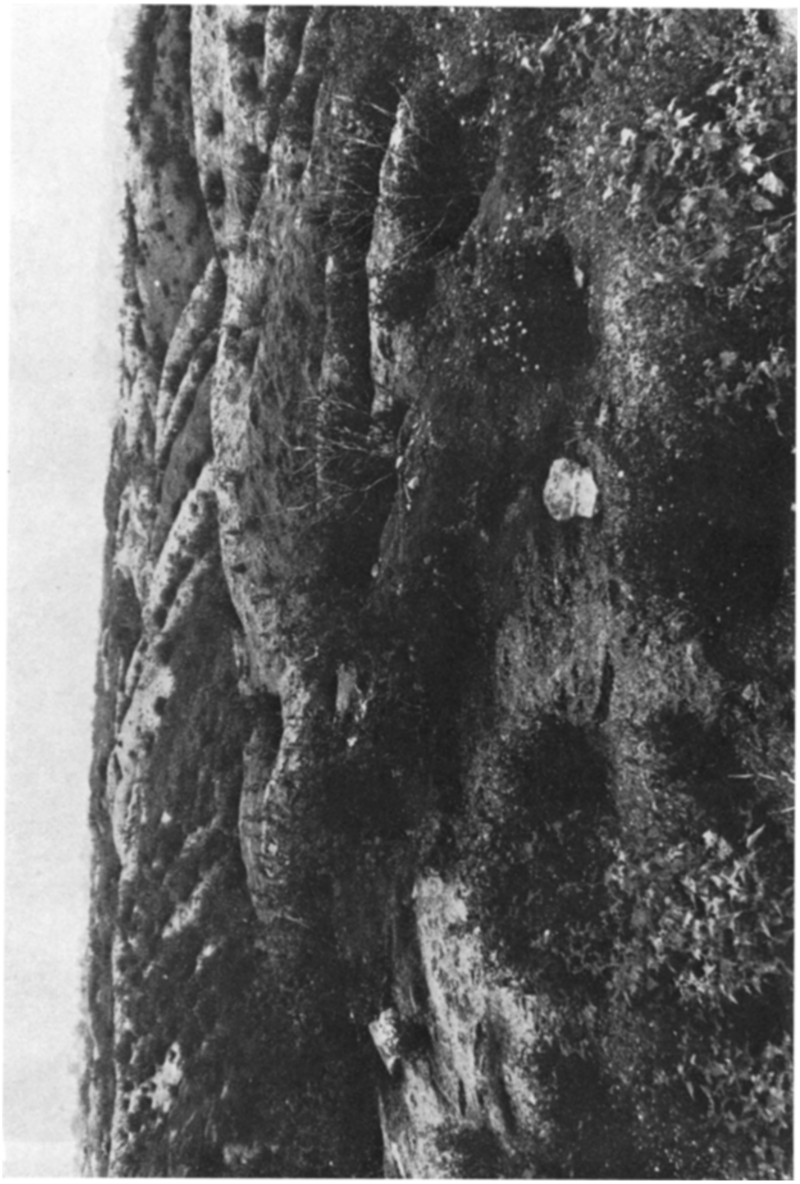
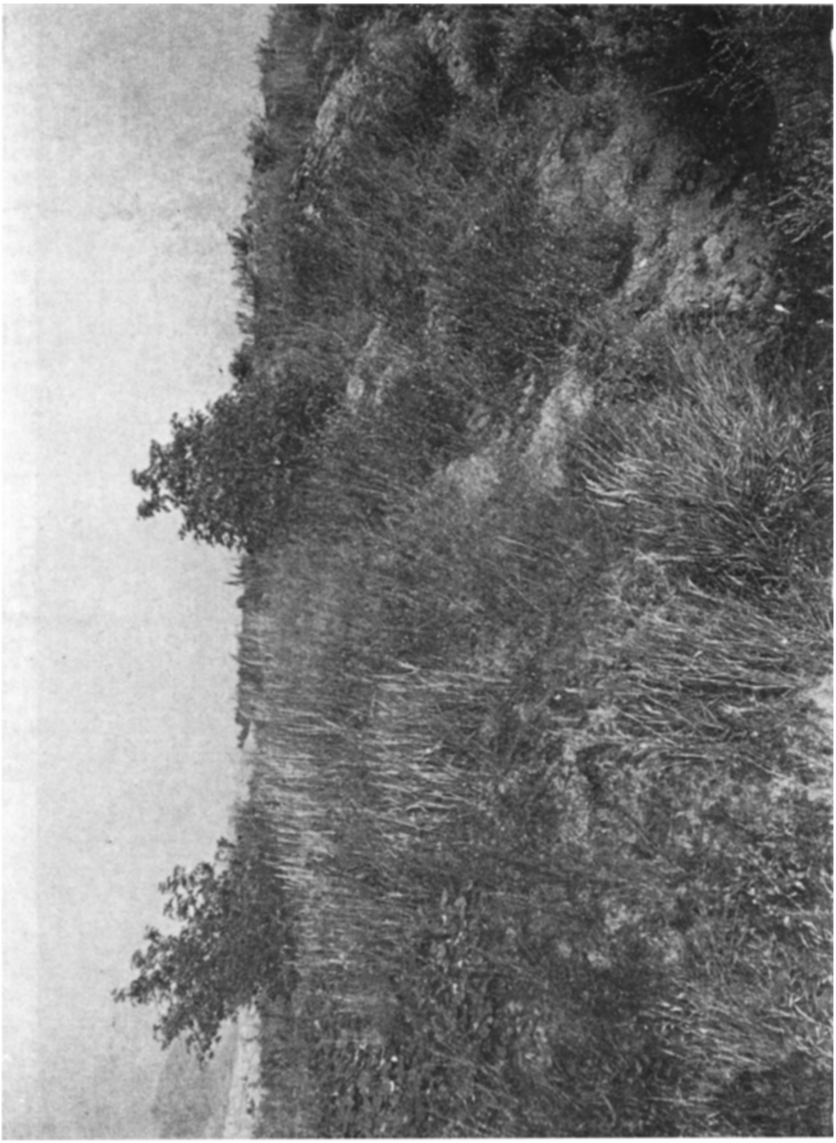
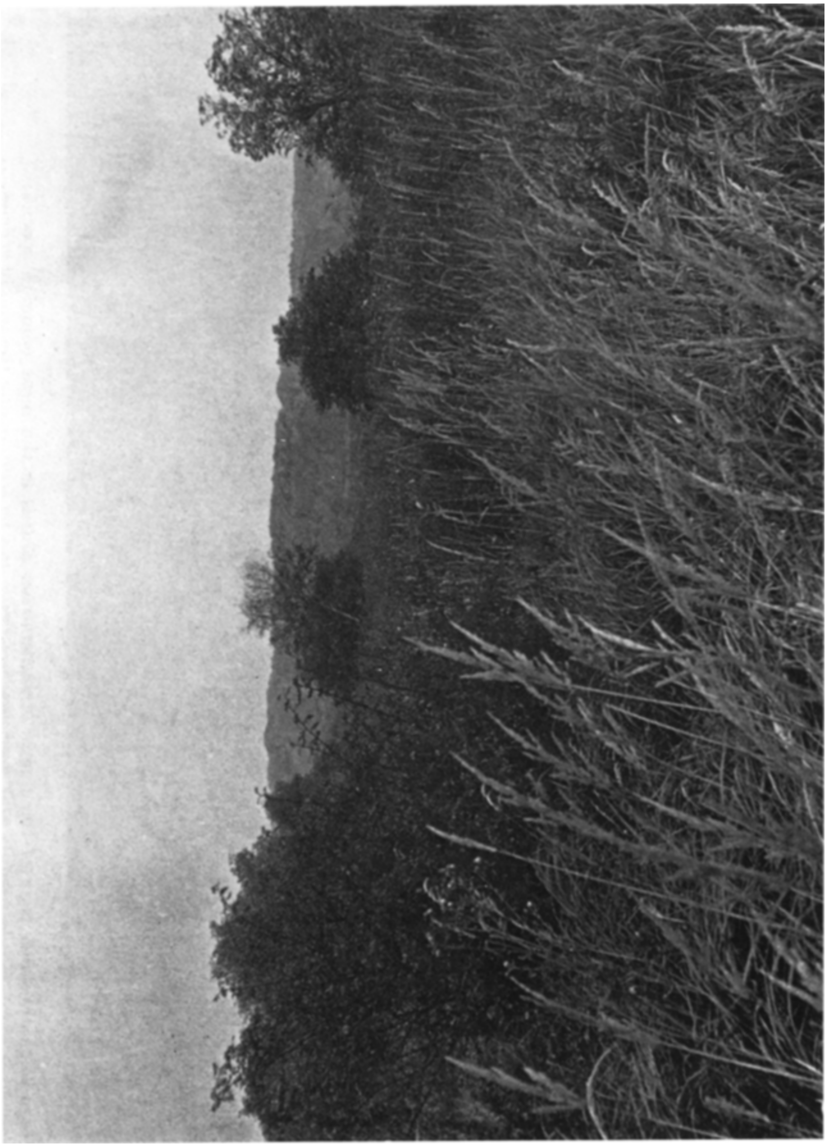
Plates 7—10



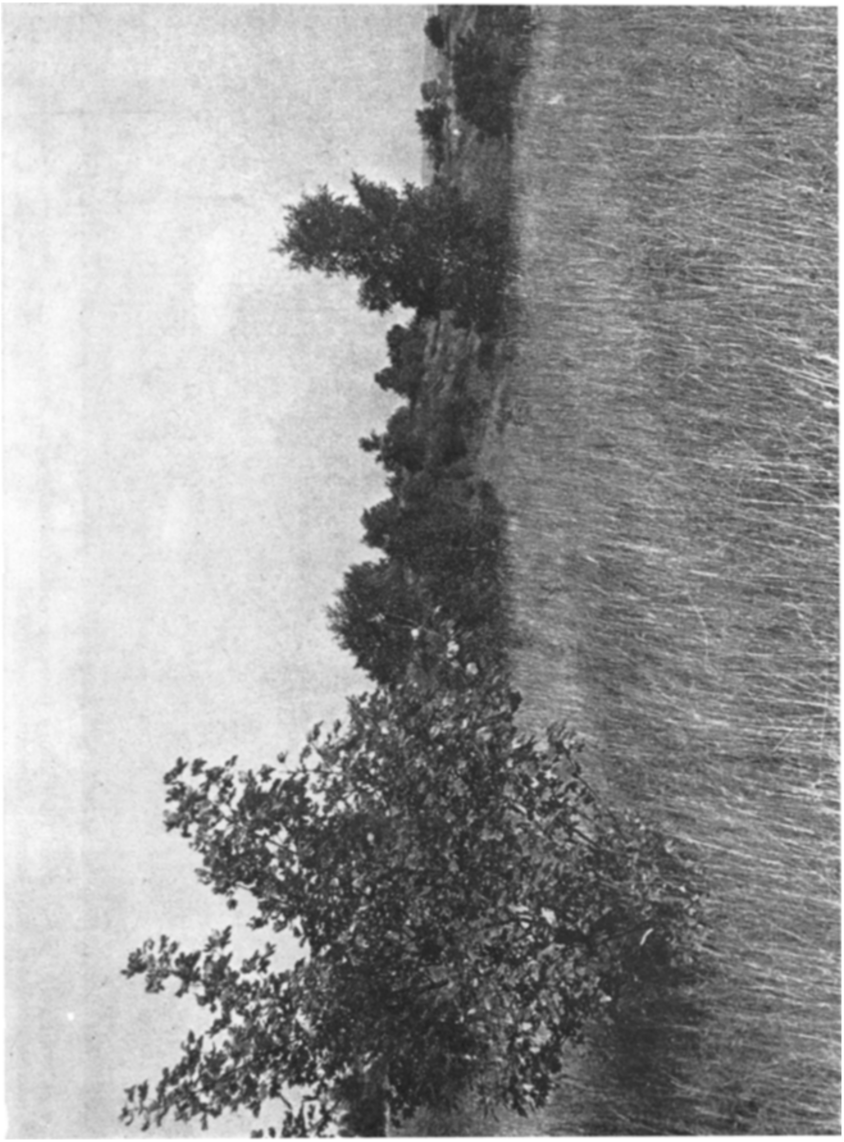
Stage B in the 2nd year of its existence; *Polygonum lapathifolium*, *Senecio viscosus*, and *Atriplex nitens* were the commonest species.



A part of Stage A in the 8th year of the dumps covered with *Carduus acanthoides*, *Tussilago farfara*, *Artemisia vulgaris*, *Calamagrostis epigejos*, *Sambucus nigra*, etc.



Stage C in the 18th year of the dumps covered with *Calamagrostis epigejos*, *Arrhenatherum elatius*, *Tanacetum vulgare*, *Rosa canina*, *Sambucus nigra*, etc.



Stage D in the 30th year of the dump. *Arrhenatherum elatius* is the most common species; *Sambucus nigra*, *Betula pendula* and *Acer pseudoplatanus* can be seen among the woody species.