VEGETATION SUCCESSION OVER AN AREA OF A MEDIEVAL ECOLOGICAL DISASTER. THE CASE OF THE BŁĘDÓW DESERT, POLAND

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Summary: The Błędów Desert in the southern part of Poland is an extensive area of sands and gravels. The origin of the desert had nothing to do with climatic conditions: The effective cause was the development of a major mining and metallurgical industry that started in the 13th century. The surrounding forests were the main fuel source for the industry. In second half of the 20th century, the ca. 18 sq km desert was one of the largest inland areas of blown sand in Central Europe. Based on the analysis of maps from 1804, 1911, 1914 and 1933 and of aerial photographs taken in 1955, 1973 and 1996, changes in the landscape of the Błędów Desert area and in the outline of permanent and drift sands were estimated, as was the gradual overgrowth of the area. The study shows that over ca. 200 years, the vegetation succession in the desert occurred in primary and secondary ways and that it can be divided into 9 phases that are grouped into 3 stages. The primary succession took place in areas covered by loose, bare sand, the secondary succession in areas with remnants of fossil soils. The essential ecological and environmental importance of an initial phase involving algae and cyanobacteria was investigated. This involvement facilitated colonisation by species with high ecological requirements through the fixing of loose sands, moisture absorption and the retention and improvement in edaphic conditions. Up to now, such a phase has not been described in terms of species composition and habitat, but this was done in this study.

Zusammenfassung: Die Błędów Wüste im südlichen Polen ist ein ausgedehntes Sand- und Kiesgebiet, dessen Entstehung und wüstenartiger Charakter allerdings nicht auf klimatische Bedingungen zurückzuführen ist. Der Ursprung dieser Landschaft steht vielmehr im Zusammenhang mit dem bereits im 13 Jahrhundert aufkommenden erz- und metallverarbeitendem Gewerbe. Die Holzvorräte der umliegenden Wälder bildeten die Hauptenergiequelle für diese Industriezweige. In der zweiten Hälfte des 20. Jahrhunderts war das ca. 18 km² umfassende Areal eine der größten Inland-Sanddünengebiete in Mitteleuropa. Basierend auf der Analyse von Karten aus den Jahren 1804, 1911, 1914 und 1933 sowie von Luftbildern aus den Jahren 1955, 1973 und 1996, wird anhand des Ausmaßes der Sandverwehungen sowie des graduell differenzierten Wiederbewuchses die Landschaftsveränderung in der Błędów Wüste aufgezeigt. Die Untersuchungen belegen, dass über einen Zeitraum von ca. 200 Jahren im Zuge der Vegetationsentwicklung primäre und sekundäre Entwicklungen zu beobachten sind. Die Sukzession lässt sich in drei Stufen einteilen, welche wiederum in insgesamt 9 Phasen zu unterteilen sind. Während die primäre Sukzession in Arealen mit lockerem, offenem Sand stattfindet, ist die sekundäre Sukzession auf Areale mit Relikten fossiler Bodenbildung beschränkt. Wie die vorliegenden Untersuchungen erstmals belegen, kommt in der initialen Phase der Vegetationsentwicklung Algen und Cyanobakterien eine ganz entscheidende Bedeutung zu. Durch die Fixierung des Sands und eine Steigerung des Wasserspeichervermögens kommt es zu einer deutlichen Verbesserung der edaphischen Verhältnisse und die Ansiedlung anspruchsvollerer Arten wird somit erleichtert.

Keywords: Primary and secondary succession, forest succession, sandy ecosystem, human impact

1 Introduction

The Błędów Desert is one of the most interesting landscape areas of Poland. This name is a geographical concept introduced into the literature in the second half of the 19th century to describe a vast sandy area without vegetation that resulted from extensive logging in the Middle Ages. The area has displayed the features of a typical desert landscape for 800–900 years. As a result of what was a medieval ecological disaster, an anthropogenic desert appeared in a temperate climate. A typical desert landscape remained up to the 1950s. Human interference, especially military activities that lasted from World War II until the end of 1980s, contributed to the continuity of this long history of bare sands.

Succession processes driven by human activities have been known for many years (CLEMENTS 1928). Ecologists have been recording such changes for over a hundred years. WARMING (1895) and COWLES (1901) were among the first to form concepts of vegetation dynamics by observing primary successions

on dunes. Numerous theoretical concepts of the general process and of the succession mechanism in various ecosystems have been discussed (e.g., EGLER 1954; PEET and CHRISTENSEN 1980; PICKETT et al. 1987; TILMAN 1990; FALIŃSKI 1986, 2003; FALIŃSKA 2003).

The theory of succession is one of the oldest in plant ecology and was formulated by CLEMENTS at the beginning of the 20ᵗʰ century (1916). CLEMENTS (1916, 1928) thoroughly developed the theory. The concept of succession explains the causes of succession and the mechanisms of vegetation change in time and up to now is the basis of ecological investigations. According to CLEMENTS (1928), succession is a directed pathway of vegetation change in an open site. These changes in vegetation during the succession have a progressively, ordered and predictable character. The regeneration is possible because of the specific characteristics of the vegetation during the succession. The final stage of succession is the formation of climax ecosystems. The bases of this concept are: *nudation*, which is the removal of vegetation by disturbance on a site in which succession can occur; *migration*, arrival of organisms at the open site; *ecesis*, the establishment of organisms in the site; *competition*, the interaction of organisms at the site, and *reaction*, the alteration of the site by the organisms.

CLEMENTS distinguished three main stages of succession: initial, optimal, and terminal stages. During the *initial stage*, the initiation of the succession is conditioned by occurrences of open site. If the area was not colonized by vegetation, the succession has primary character. During the colonization of open sites, a significant role is played by the migration of propagules in cases of primary succession and soil seed bank in cases of secondary succession. The *optimal stage* of succession is conditioned by relations between biotic and abiotic components of environment, especially the influence of vegetation on physical and chemical properties of soil. The *terminal stage* of succession is the final period of stabilized plant community formation with characteristic species composition in a given climatic zone. The concept of succession formulated by CLEMENTS was and is criticized by many ecologists, but is still the basis of many models of successions proposed in the 20ᵗʰ century (PICKETT et al. 1987).

Spontaneous succession in the area of the Błędów Desert took place according to the classic succession model (CLEMENTS 1916), the mechanisms of plant competition for nutrients model of TILMAN (1990) and the model of facilitation (CONNELL and SLATYER 1977). Facilitation is the process whereby early succession species occupying a terrain facilitate habitat conditions for the late succession species. In the process, the place of one species is replaced by other species. Facilitation has long since been considered a driver of ecological succession (CLEMENTS 1916). However, this hypothesis has been questioned (DRURY and NISBET 1973; CONNELL and SLATYER 1977) as experimental studies indicated that early succession species inhibit rather than facilitate the introduction of late succession species (ARMESTO and PICKETT 1986; WALKER and CHAPIN 1986). However, as the majority of these studies were carried out in environments rich in resources and with well-developed soils, the facilitation mechanism probably did not play a significant role (WALKER and CHAPIN 1987). It is accepted that the facilitation model is an important succession mechanism in severe and extreme environments, where occupying plants increase the nutrient availability to the level required by the late succession plants (CONNELL and SLATYER 1977; TILMAN 1985, 1990). Low levels of nutrients (WALKER 1999) and their reduction by plant growth (DEL MORAL and WOOD 1993) are the factors limiting colonization in the early phase of primary succession. Because the Błędów Desert is characterized by extreme habitat conditions, the succession processes take place mostly by way of facilitation as in other sandy areas (PRACH 1989).

As suggested by BERGER-LANDEFELDT and SUKOPP (1965), ELGERSMA (1998), and JENTSCH and BEYSCHLAG (2003) and others, the course of succession and development of various species colonising sandy areas depends on climatic factors, soil pH, water availability, substratum type and its fertility, and availability of nutrients. However, the most significant factor is the scale of human disturbances related to the destruction and complete degradation of the soil cover that, especially in sandy ecosystems, play a key role in influencing the rate of succession.

The dynamics of open ecosystems, especially psammophilous grasslands in Europe, were mainly sustained by human land use (TÜXEN 1960). Forests were clear-cut or logged and cattle and sheep were grazed on meadows. During the last few centuries, extensive sheep pasturing and military activities were the most intensive ways of using land; Thus, acid grasslands and heathlands were retained (CZYŻEWSKA 1992). Currently, dry acid psammophilous grasslands, dominated by *Corynephorus canescens,* are threatened with extinction over much of Europe due to vegetation succession. In military training grounds, there are still minor habitats with plants once common in Europe; the Błędów Desert may

be an example. Habitats are being increasingly destroyed by urban expansion and changes in land use. The dry and wet deposition of atmospheric nitrogen, and other factors, has accelerated the decline of psammophilous grasslands.

The development and functioning of open sandy ecosystems has inspired many studies on the ecology and dynamics of xerothermic and psammophilous plants (Jentsch and Beyschlag 2003). Most concentrated on the species content and course of succession within the range of continental psammophilous grasses in both semi-natural and anthropogenic habitats (Jentsch et al. 2002). Aerial photography has also been used to study the course of the successions in anthropogenic habitats (Olson 1958; Falińska 2003).

Detailed studies of the succession in the Błędów Desert, especially thorough geobotanic analyses, have not been carried out to date. The first general field investigations were by Szczypek et al. (1994), who mapped changes in vegetation layout using aerial imagery. However, the latter work does not thoroughly discuss the process of succession of psammophilous vegetation in the area. Hence, the aim of this work is to (a) study the mechanisms and past and present rates of succession, (b) evaluate the role of primitive organisms on the initiation of the succession and (c) define the influence of natural and anthropogenic factors on the succession.

2   Materials and methods

2.1 Maps and aerial imagery

Maps and aerial images were used to analyse the course of the vegetation succession. These enabled analysis of changes in sand distribution and vegetation cover over a period of almost 200 years.

Old maps provide valuable information on the evolution of the geographical environment; they were crucial to this investigation of the Błędów Desert. When determining changes over time, map accuracy had to be confirmed by comparing selected elements in both old and contemporary maps. The old maps are on different scales and involve different levels of generalisation and various cartographic techniques. However, they are the only sources of information on the vegetation succession and its tempo after the medieval clear-cutting of the forests.

Cartographic information was obtained from the following sources: A topographic map of Western Galicia by A. Mayer von Heldensfeld 1801–1804 (scale 1:28 800); Military Institute of Geography in Vienna of 1911 (1:200 000); Map of western Russia 1914 (1:100 000); Polish map published by Military Institute of Geography in 1933 (1:100 000). Black and white aerial photographs of the desert taken in 1955 and 1973 (1:17 870) and colour photographs taken in 1996 (1:16 580) were also used.

GIS methods were used in the analysis and interpretation of the maps (Longley et al. 2005). Analogue maps and serial photographs were scanned, registered in the Cartesian coordinate system and unified with respect to scale as the source material used was derived from different times and was made in different ways. The program MapInfo 7.8 was used to make an interpretative sketch map by vectorizing analogue source materials (Longley et al. 2005) to show vegetation patches, ploughed lands, pastures, built-up areas and boundaries of the Błędów Desert area. The geographic sizes of particular landscape components were measured. This map was the basis for interpreting and evaluating changes in the landscape.

2.2 Vegetation

Field investigations on the course of the succession were carried out in 11 consecutive vegetation periods (1994–2005). To register the actual state of vegetation and to determine and explain the natural vegetation succession, four research transects of a fragment of the Błędów Desert were defined (Fig. 1).

The four transects involve a total length of 7650 m and cover an area of 153 000 m². They represent different stages of the vegetation succession from the primary active-deflation fields to the final sod-covered habitats and pine coniferous forest. The stages of succession were distinguished on the basis of field observation, the degree of sand stabilization and type of vegetation (grassland, shrubs, initial forest, forest). The transect names derive from the places delimited: I – Między Bunkrami (3300 m x 20 m), II – Źródlisko Białej (1300 m x 20 m), III – Centuria (1600 m x 20 m) and IV – Przełom (1400 m x 20 m). Transects were delimited using geodetic methods and their courses marked by cement piles placed every 100 m. As they are permanently marked, they will be useful in future studies. These areas are included in the detailed 1:500 schemes showing the vegetation distribution in particular sandy habitats characterized by different degrees of fixation. The degree of sand fixation was the criteria used in locating the transects.
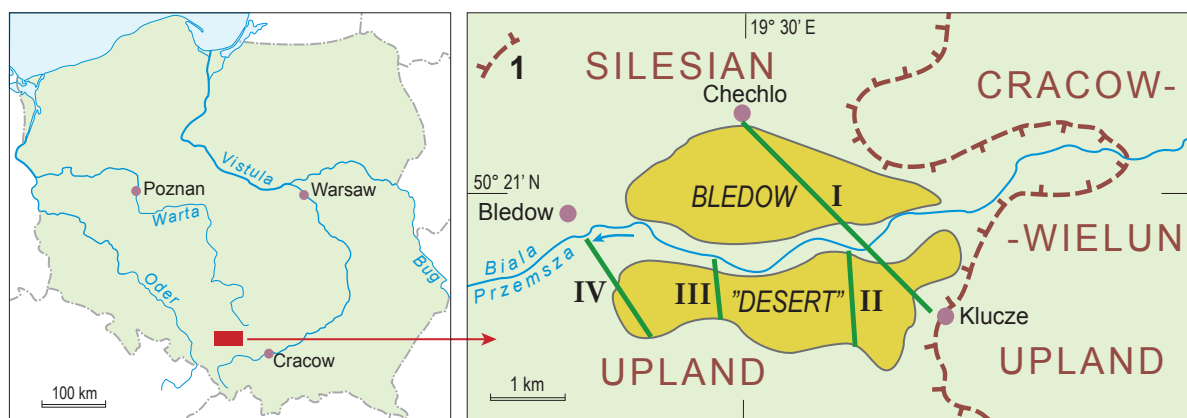
Fig. 1: Location of the Błędów Desert and transects. 1 – course of Upper Jurassic cuesta; I – Między Bunkrami; II – Źródlisko Białej; III – Centuria; IV – Przełom

Many phytosociological surveys were undertaken in the four transects using Braun-Blanquet's method (Fukarek 1967). In forest communities, the surveyed areas were 100-200 m² whereas, in psammophilous swards, the areas of patches studied fluctuated between 4–20 m². Out of a total of 105 surveys, 83 formed the basis for distinguishing associations at particular stages of succession. The types of plant associations were determined on the basis of characteristic and differential species. Species belonging to specific syntaxonomic groups were determined according to the classification of Matuszkiewicz (2001).

The cryptogamous and vascular plant species representing different phases and stages of succession were listed in the form of floristic list. During the field-works the individual species of plants were recognized and collected for herbarium. The identified material of algae and cyanobacteria was taken to the laboratory culture in Petri dishes. Live material was used to identify the species. The participation of particular species to given phases of succession was determined by their frequency of occurrence in a given phase and stage of vegetation succession and literature data for similar sandy ecosystems areas (Faliński 1986; Czyżewska 1992; Faliński et al. 1993 and others). This helped in providing an overview of the course of the succession and in determining the contribution of particular species and their transition to later phases of the succession. Latin names of vascular plants are from Mirek et al. (2002), of lichens from Santesson (1993) and of mosses from Ochyra and Szmajda (1992).

Species of algae and cyanobacteria were identified by analysing live material collected from 17 sites. A scanning electron microscope Philips XL 30

ESEM was used. Observations were also made of the surface of the algal cover on the sand substratum and of single sand grains covered with algae cells.

3 The origin of Błędów Desert landscape: a medieval ecological disaster

The Błędów Desert is located in the eastern part of the Silesian Upland in the vicinity of the Upper Jurassic cuesta of the Cracow-Wielun Upland (Fig. 1). An accumulation of mainly Pleistocene sands and gravels, 60–70 m thick, belongs to the Odranian (Riss) and the Vistulian (Würm) glaciations (Szczypek and Wach 1989). These deposits are mostly of riverine-extraglacial or riverine-prolluvial origin. The area of the Cracow-Wielun Upland, where fluvioglacial material had accumulated during the Sanian glaciation (Mindel), was their source. The deposits were transported from there to fill a system of deep pre-Quaternary valleys (Szczypek and Wach 1989; Pelka-Gosciniak et.al. 2007). The sands and gravels were later mixed with local weathering material from Upper Jurassic limestone and ore-bearing dolomite. The weathered material occurs as intercalations and on the surface in the area and because of increasing nutrient sources, is of significant importance to the vegetation succession and soil development. The weathered Jurassic material was an additional source of nutrients that fertilized the very poor sandy habitat. It caused the acceleration of vegetation succession that influenced the development of soils.

From the beginning of the Holocene, the Błędów Desert was covered by a dense mixed forest where, in the subboreal period (5100 BP), pine trees began to dominate (Szczypek et al. 1994). This

was the situation up to the beginning of the Middle Ages when ore mining and processing led to the forests being destroyed, exposing vast areas of sandy rock. Degradation of the soil cover destroyed the local flora and fauna. This was a medieval ecological catastrophe.

Shallow Triassic rocks, mostly dolomites containing lead-zinc ores, were easily accessed for medieval exploitation. Thus, the area became one of the first in Poland where industrial activity led to serious environmental damage. The history of mining in the area has been told many times (e.g., Molenda 1963); all ascribe the arid character of the area to human economic activity. Very little notice was taken at that time of environmental disturbances.

It is known that the ores had been exploited for lead in the first half of the 13th century. Charcoal was the basic fuel of the medieval metallurgical industry. Coal was not exploited in Poland before the end of the 18th century. A large number of trees were logged as a result. Timber was also used for building wooden adits. As the ore mining industry developed, the demand of timber increased greatly. By the end of the 16th century, old adit support timbers were being re-used; new wood was clearly already scarce at that time. The increasing demand is also indicated by the requirements listed by clerks from the Sztolnia Ponikowska (Ponikowska Adit) in 1563 which details the amount of oak wood used in a 100 m adit, namely, 600 pieces for supports, 3000 for passages, 120 for covers and separators and 300 for wooden shingles. Timber was also required for wheels, axles, wheelbarrows and shaft-covering roofs. Truly, forests vanished in mines (Czaja 2001) – the history of the Błędów Desert had begun.

Forest exploitation also had a negative influence on soil quality. Clear-cutting resulted in the removal of thin layers of humus and the excavation of deeper parts. Livestock grazing probably also helped to degrade the soil cover. Damage to the soil-protecting natural vegetation permitted loose sand that had been eroded from the rock below to appear on the surface. Vast deflation fields formed that hindered vegetation growth. This was the character of the area for hundreds of years (Fig. 2A). Fields of bare sand remained up to the end of World War II. Afterwards, the area was used as an army testing ground. No scientific investigations were allowed as military activities contributed to maintaining the desert-like character of the area. Not for the first time, W and SW winds played the key morphogenetic role as they created the great deflation surface of the Błędów Desert – an anthropogenic desert landscape.

Unfortunately, 25–30 years ago when the desert-like landscape was an extraordinary feature covering about 34 km², no one paid attention to its unique and unusual character. However now, the desert-like landscape covers only about 22.5 km² and, with human activity decreasing, the entity that was desert has almost disappeared; remaining areas without vegetation range from several dozens of hectares to a little over 1 km². It has become obvious what has been lost (Szczypek et al. 2001; Rahmonov 2007). By making motocross tracks, horse riding trails and walking paths, attempts are being made to draw tourists to what remains of this unique landscape even as it vanishes due to a high rate of vegetation growth.

4 Results

The vegetation dynamics in the area of the Błędów Desert is characterized by secondary and primary types of succession, clearly visible on maps and in aerial photos. Areas with primary successions occur in the SE over still-active deflation fields and loose bare sands.

4.1 Vegetation dynamics in the period 1804-1996 from maps and aerial imagery

The results of the analysis of vegetation changes and of the distribution of permanent and drift sands over 200 years are summarized in table 1. The area has been gradually overgrown, first by scattered clumps of shrubs and trees and later by continuous forest.

The areas covered by herbaceous vegetation, shrubbery and trees were delineated over 11 years in the field and by analysis of the aerial photographs taken in 1994 and 1996 (Tab. 1). Precise analyses of the aerial photographs taken in 1955 and 1973 provided the basis for estimating the sizes of areas gradually colonised by vegetation during natural succession and by the forced anthropogenic succession in the form of planting and cultivation.

In 1955, the Błędów Desert was a huge deflation area with W and NW limits defined by dune ridges (Fig. 2A). The 1973 aerial imagery shows significant changes in the dynamics of vegetation, both natural and anthropogenic (Fig. 2B). Vast areas of the deflation basin in the northern and southern parts of the desert had changed significantly. Alternate plantings of coniferous and deciduous

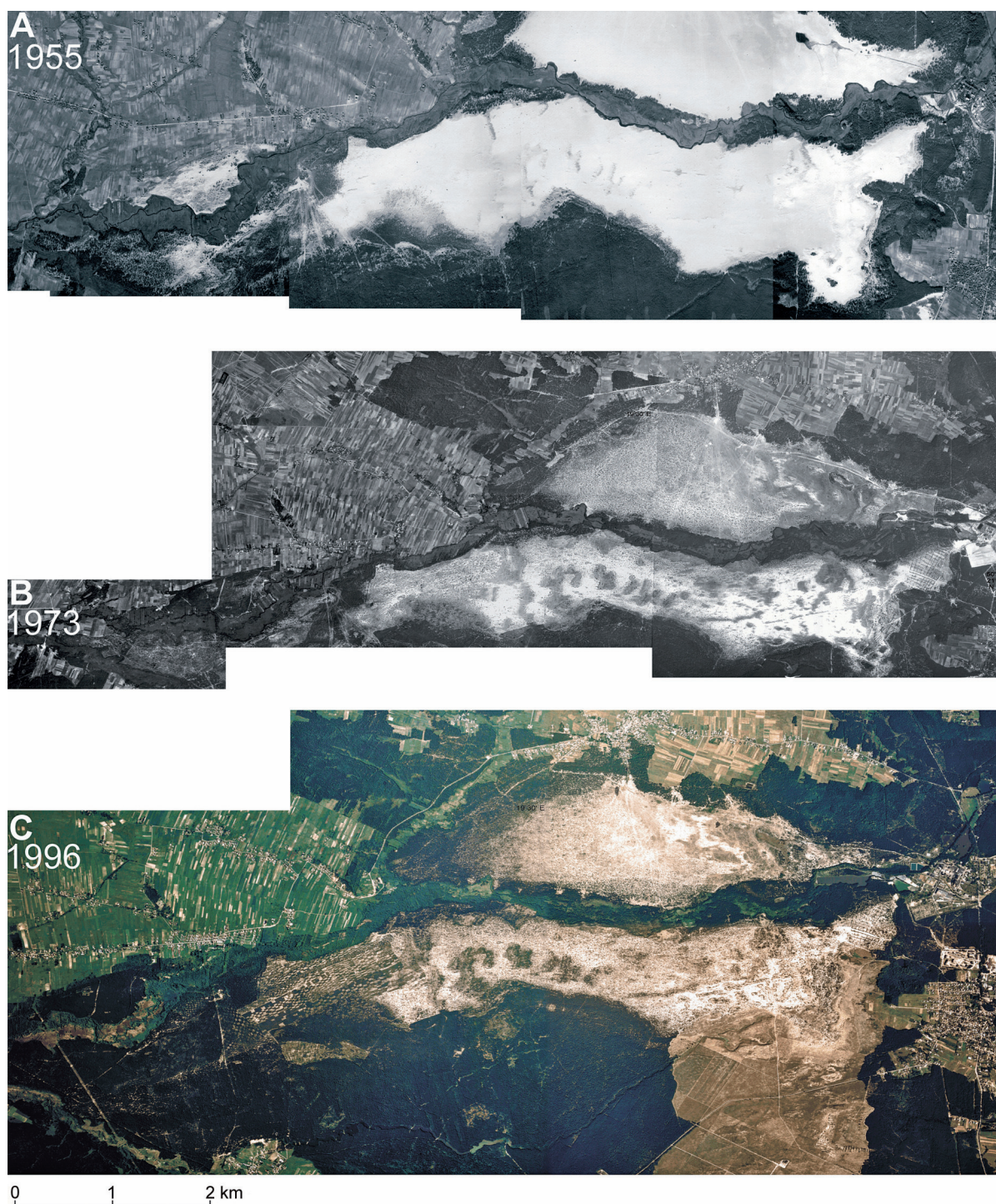Fig. 2: The Błędów Desert and its neighborhoods on aerial photographs: A – as in 1955; B – as in 1973 and C – as in 1996

trees, reflected in a characteristic checkerboard pattern in the 1996 imagery (Fig. 2C, 4C), shows the importance of human activity in the secondary vegetation succession.

4.2 Succession stages and phases

The degree of sandy-ground fixation was the basic criterion used to establish specific stages of

Tab. 1: Changes in the range of vegetations in the Błędów Desert from 1804-1996

Vegetation and other elements of landscape	Interpretations made from maps								Interpretations made from airphotos					
	1804		**1911**		**1914**		**1933**		**1956**		**1973**		**1996**	
	[km²]	%	[km²]	%	[km²]	%	[km²]	%	[km²]	%	[km²]	%	[km²]	%
Sand areas with no vegetations	**19,2**	52	**13,4**	36	**16,1**	43.6	**15,2**	41.3	**11,3**	30.6	**2,2**	6.0	**0,3**	0.9
Initial grasses of *Corenyphorus* and *Koeleria*									**0,8**	2.2				
Grasses of *Corenyphorus* and *Koeleria*											**2,6**	7.1	**0,9**	2.4
Grasses of *Corenyphorus* and *Koeleria* continuously destroyed by human impacts													**1,4**	3.8
Corynephorus grasses with biogroups in various degree of development									**1,2**	3.3	**1,2**	3.3	**2,6**	7.1
Community with domination of *Salix acutifolia* in complex with *Corenyphorus* and *Koeleria* grasses											**2,7**	7.3		
Community with domination of *Salix arenaria* in complex with *Corynephorus* and *Koeleria*											**2,6**	7.2		
Shrubs of willow-birch-aspen-pines													**0,6**	1.6
Forest areas	**10,5**	28	**13,1**	36	**16,1**	43.7	**15,6**	42.3						
Initial fresh pine coniferous forest													**1,3**	3.5
Initial fresh pine coniferous forest with scattered tree stand									**4,9**	13.3			**0,5**	1.5
Fresh pine coniferous forest									**12,3**	33.3	**16,2**	44.0	**15,1**	40.9
Beech and mixed forests									**0,2**	0.5	**1,1**	3.0	**1,2**	3.2
Additional plantation within natural pine forest											**2,2**	6.0		
Artificial plantation of *Pinus sylvestris, P. nigra, P. strobus, Betula pendula, Alnus glutinosa, A. incana, Quercus rubra*													**5,3**	14.3
Plantation of *S. acutifolia*											**0,4**	1.1	**0,3**	0.7
Riverside carrs and hygrophilous communities	**2,0**	5	**4,4**	12	**1,6**	4.3	**2,3**	6.2	**2,6**	7.1	**2,3**	6.2	**3,1**	8.3
Water reservoir							**0,4**	1.0					**0,2**	0.6
Arable field, pasture and buildings	**5,2**	14	**6,0**	16	**3,1**	8.4	**3,4**	9.2	**3,6**	9.8	**3,3**	9.0	**4,1**	11.2
Total:	**36,9**	100	**36,9**	100	**36,9**	100	**36,9**	100	**36,9**	100	**36,9**	100	**36,9**	100

the succession and their phases. The initial stage involves non-stabilized ground. In the optimum stage, the surface is consolidated with shrubbery. With transformation of the shrubbery towards forests, the terminal stage of succession is formed pine forests.

Three stages and 9 succession phases (0–8) were distinguished by a comparison method partially verified, for the initial phases, by imagery interpretation and by observations over 11 years on the 4 transects. Transects I, II and III differ in their plant communities as compared with transect IV (Tab. 2). Transect IV is characterized by the degree of substratum fixation and a much smaller area (or lack) of tree plantings. Transects I-III, in comparison, are characterized by the degree of sand fixation and smaller surfaces with planted trees.

From the investigations carried out, the artificial plantings are of essential importance in the accel-eration of the succession rate. An absent or reduced deflation surface with algae (Tab. 2) reflects an advanced stage of succession and a lessening of winds hindering the introduction of vegetation.

4.3 Primary succession

The natural series of the primary succession starts with algacenosis followed by psammophilous grasses of the *Koelerio glaucae-Corynephoretea canescentis* class, especially from unions of *Corynephorion canescentis* and *Koelerion glaucae*. Deriving from these unions, a single species of trees with shrub forms gradually overgrew the area. These formed later biogroups that, at the optimum stage, became pine forests (*Leucobryo-Pinetum*) belonging to a *Dicrano-Pinion* (Fig. 3) union.

Tab. 2: The vegetations on the transects I-IV

Plant communities	The participations of plant community on the transects							
	I – Między Bunkrami		II – Źródlisko Białej		III – Centuria		IV – Przelom	
	[m²]	[%]	[m²]	[%]	[m²]	[%]	[m²]	[%]
Deflation field with *Algae* and *Cyanophyta*	8,170	12.35			1,015	3.17		
Spergulo morisonii-Corynephoretum canescentis subass. *cladinetosum mitis*	1,150	1.77	415	1.59	225	0.7	-	-
Grasses of *Elymus arenarius*	1,780	2.71	370	1.22			-	-
Festuco-Koelerietum glaucae with willow-birch shrubs - biogruops	17,800	27.32	7,375	28.40	12,053	37.76	-	-
Community with domination of *Salix acutifolia*	1,490	2.26	6,920	26.63	634	1.98	-	-
Community with domination of *Salix arenaria*			2,080	8.00	-	-	-	-
Scattered tree stand of *Pinus sylvestris*	1,700	2.57	1,870	7.37	-	-	-	-
Brush of *Populus tremula*	5,150	7.86	1,840	7.07	-	-	-	-
Leucobryo-Pinetum – initial stage	1,950	2.95	3,050	11.72	865	2.70	-	-
Leucobryo-Pinetum – terminal stage	5,590	7.63	2,080	8.00	6,185	19.31	16,690	57.56
Leucobryo-Pinetum with additional plantation	3,600	5.45	-	-	-	-	12,310	42.44
Cladonio-Pinetum	2,910	5.65	-	-	1,177	3.67	-	-
Artificial trees plantation	14,710	21.48	-	-	9,846	30.71	-	-
Total	**66,000**	**100**	**26,000**	**100**	**32,000**	**100**	**29,000**	**100**

4.4 Initial stage

Phase 0. Bare sand on the surfaces of the deflation fields and the accumulated aeolian sediments are inhabited by soil algae and cyanobacteria (Fig. 3). The cyanobacteria are represented by *Chroococcus minor, Ch. minutus, Ch. varius*, and the algae by *Pinnularia borealis, Stichococcus chlorelloides, Klebsormidium crenualtum* and *Cylindrocapsa* sp. (Suppl. I). Slow encroachment of mosses such as *Polytrichum piliferum, Ceratodon purpureus* and *Rhacomitrium canescens* is found in areas previously colonized by the algae. The initiation and course of the succession remained under the influence of the input stage – the character of the soil and vegetation. The biocenotic role of the latter cryptogam species involved the initiation of sand fixation, humidity accumulation and maintenance.

Phase 1. This phase commences in three ways (Fig. 3) and varies in manner of settling. Plant colonisation into areas settled by algae and cyanobacteria is the common feature. *Stichococcus. cf. fragilis* and *Gloeocapsa atrata* appear, in addition to algae and cyanobacteria, at this stage. Some cyanobacteria retreat.

The first manner of colonization involves mass encroachment of cryptogam species and the appearance of vascular species such as *Corynephorus canescens, Cardaminopsis arenosa, Carex hirta, Rumex acetosella, Hieracium pilosella, Elymus arenarius, Jasione montane, Cerastium semidecandrum* and single individuals of *Koeleria glauca* (Suppl. I). *C. canescens* is the dominant species among the vascular plants. *E. arenarius*, the next most important early succession species, begins the process of sand stabilization by vegetation overgrowth. *Polytrichum piliferum* forms large surface patches, mostly with male and partly with female specimens. There are no vascular plants in this consolidated moss turf.

The second manner of colonisation involves lichens, especially of genus *Cladonia* and single specimens of others (Suppl. I). They occur both on the surface of sand covered with algae (which may be invisible in summer) and within areas of *Corynephorus* grass and *P. piliferum* patches. There are also species present such as *Stereocaulon condensatum, S. incrustatum, Diploschistes muscorum, Cladonia cornuta, C. glauca, C. fimbriata, C. uncialis, C. cervicornis* ssp. *verticilata* and others. These species, at later stages, colonise *P. piliferum* patches and destroy them.

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                                   │                                        │
                                   ▼                                        ▼
                    ┌──────────────────────┐                  ┌──────────────────────┐
                    │ 0 Algae and          │                  │ 0 Artificial         │
                    │   Cyanophyta         │                  │   plantation         │
                    └──────────────────────┘                  └──────────────────────┘
```

Fig. 3 flowchart:

- **Sand** → **0** Algae and Cyanophyta; and Sand → **0** Artificial plantation
- **0** Algae and Cyanophyta → **1** *Salix arenaria Salix acutifolia*; → **1** *Spergulo morisonii-Corynephoretum canescentis* typicum; → **1** *Polytrichum piliferum*
- **1** *Salix arenaria Salix acutifolia* → **2** Shrubs: *S. arenaria* i *S. acutifolia*
- **1** *Spergulo morisonii-Corynephoretum canescentis* typicum → **2** *Spergulo morisonii-Corynephoretum canescentis cladinetosum* mitis
- **1** *Polytrichum piliferum* → **2** Community with *Polytrichum piliferum* + porosty z rodz. *Cladonia*
- **2** *Spergulo morisonii-Corynephoretum canescentis cladinetosum* mitis → **2,3** *Festuco-Koelerietum glaucae*
- **2** Community with *Polytrichum piliferum* + porosty z rodz. *Cladonia* → **2,3** *Festuco-Koelerietum glaucae*; → **2,3** biological soil crusts
- **2,3** biological soil crusts → **2,3** *Festuco-Koelerietum glaucae*
- **2** Shrubs: *S. arenaria* i *S. acutifolia* → **4,5** Community of willow-birch-aspen-pines
- **2,3** *Festuco-Koelerietum glaucae* → **3,4** Willows with *Festuco-Koelerietum glaucae*
- **2,3** biological soil crusts → **3,4** Willows with *Festuco-Koelerietum glaucae*
- **3,4** Willows with *Festuco-Koelerietum glaucae* → **4,5** Community of willow-birch-aspen-pines; → **5, 6, 7** Community of pine-willow-juniper-birch
- **4,5** Community of willow-birch-aspen-pines → **5, 6, 7** Community of pine-willow-juniper-birch
- **5, 6, 7** Community of pine-willow-juniper-birch → **7** Initial fresh pine coniferous forest
- **7** Initial fresh pine coniferous forest → **8** *Cladonio-Pinetum*; → **8** *Leucobryo-Pinetum*
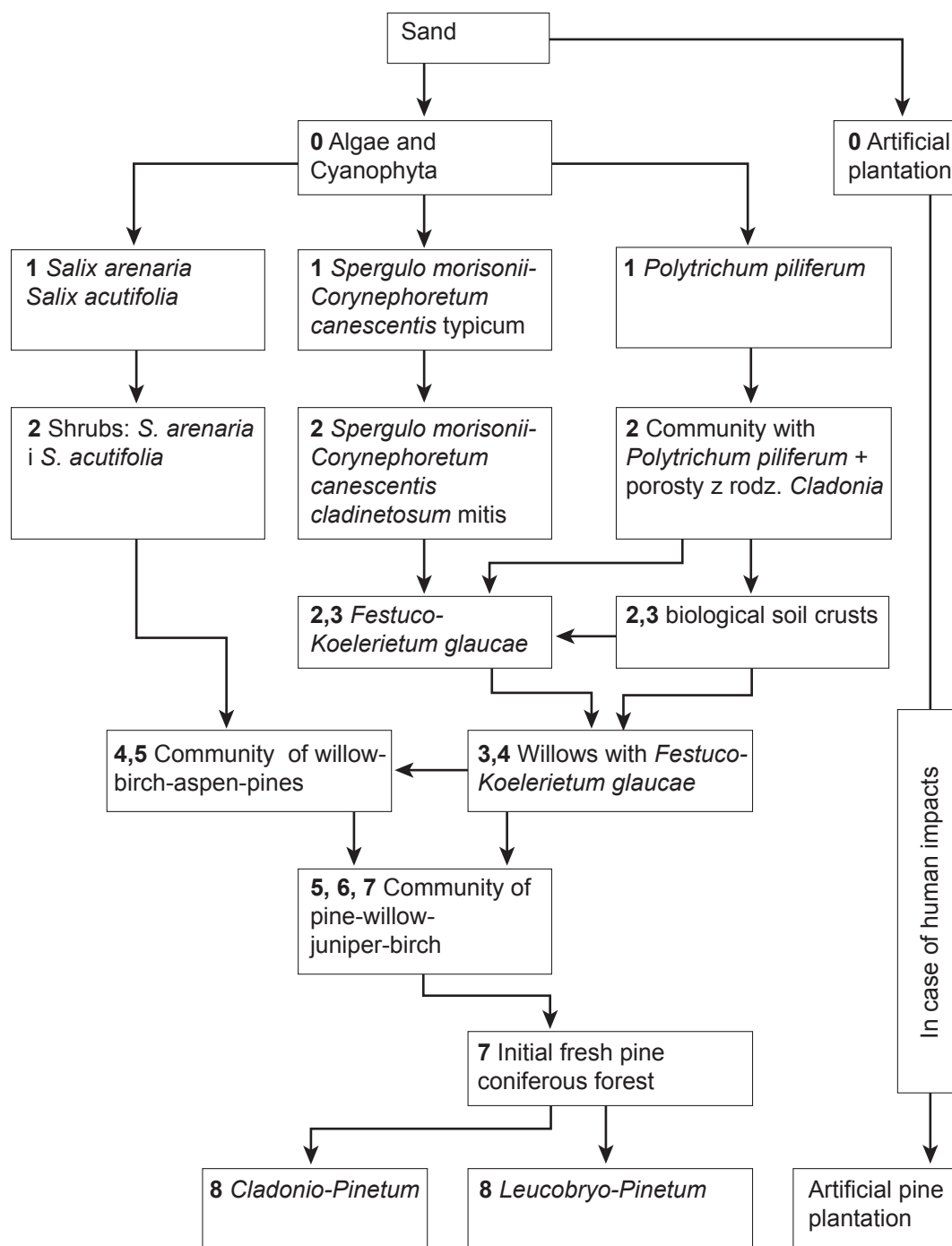- **0** Artificial plantation → In case of human impacts → Artificial pine plantation

Fig. 3: The course of the succession in the Błędów Desert

The third manner of sand colonisation involves the single shrubs *Salix arenaria* or *S. acutifolia* (Fig. 3) that, over the years, increase their canopies and consolidate the sand. Microhabitats with a specific microclimate occur underneath and support settling by other species, which initiates the formation of willow-pine-juniper-birch communities.

Phases 2 and 3. These phases involve the formation of specific communities of cryptogams and lead to the development of the so-called biological soil crust. It was mainly species from the *Algae* and

Cyanophyta groups, mosses with *Polytrichum piliferum, P. juniperinum, Ceratodon purpurea* and lichens of the *Cladonia* genus that took part in the formation of this crust in the Błędów Desert. Algal crust with *Cylindrocapsus* sp. restrains eluviation, deflation and stabilises the ground (Photo 1A, B).

The *Spergulo morisonii-Corynephoretum canescentis* sub-association of the *cladinetosum mitis* group dominates in these phases. They are preceded by a gradual colonisation of a significant number of lichen species including *Cladonia foliacea, C. glauca, C. furcata, C. cariosa, C. chlorophaea, C. pyxidata, C. floerkeania, C. fimbriata, C. gracilis, C. subulta* and *Cladina mitis, C. arbuscula* and *Coelocaulon aculeata*. Among spermatophytes, apart from those from phase 1, other taxons such as *Jasione montane, K. glauca, Festuca ovina, F. psammophila, Sclerantus annuus, S. perennis, Artemisia absinthium, Trifolium arvense, Thymus serpyllum, T. pulegioides* and *Hernaria glabra* appear or increase their succession importance. Shrub and tree species also appear (Suppl. I).

4.5 Optimum stage

Phases 4 and 5. Significant changes are observed within willow-pine-birch shrubs, which comprise a biogroup. The increase in range, size and growth of shrub-tree species result in more shaded surfaces, organic enrichment of the ground and improved soil xeric conditions.

Reciprocal influences within the biogroup lead to the formation of a slightly different niche and, simultaneously, to a species change from heliophyte to skiophyte. Up to the end of the phase, most of the psammophilous species retreat and are replaced by coniferous forest species such as *Chimaphila umbellata, Deschampsia flexuosa, Orthila secunda, Pyrola minor, Vaccinium vitis-idaea, V. myrtillus* and others. Significant changes occur in bryoflora in the final phase of the stage, as coniferous forest species such as *Pleurozium schreberi, Hylocomim splendens, Hypnum cupressiforme, Dicranum polysetum, Dicranium scoparium* and *Climacium dendroides* appear. These will become a permanent component of the developing coniferous forest (Suppl. I).

Salix acutifolia or *S. arenaria* played the crucial role in the formation of a biogroup contributing to the promotion of the succession. During the stage of willow shrub development, the shaded area of the willow increased due to vegetative proliferation and both cryptogam and vascular species typical of later stages of the succession entered. The shaded areas under the canopy or close to the trunk are covered by *Cladonia* species; these occur also under *Juniperus communis*. Increase in the willow canopy caused heliophyte species to grow close to the edge of the shaded area as pine trees started growing under the willow. The trend sand – willow – pine tree – willow-pine biogroup – pine forest is one of the simple components of the succession (Fig. 3).

4.6 Terminal stage

Phases 6, 7 and 8. As the biogroups developed, they finally connected, causing the complete retreat of the heliophyte species. During the further succession, the range of tree vegetation clumps increased to such a degree that initial forest stages with a typical pine forest floor layer including *Pyrola chloranta, P. minor, P. uniflora* or *Deschampsia flexuosa* started to form.
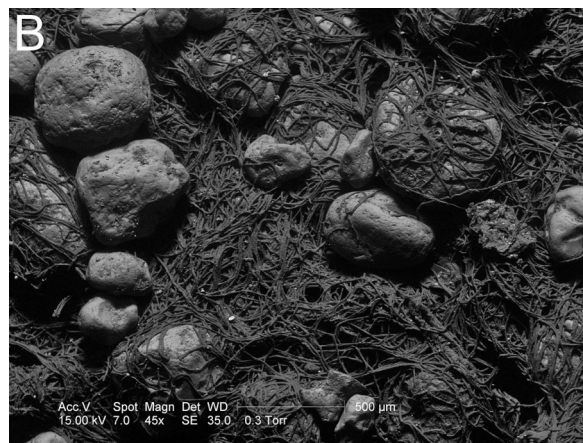

Photo 1: A – thallus fragments of filamentous alga (SEM photograph). B – algal net binding sand grains and stabilizing ground (SEM photograph)

Enrichment with other coniferous forest species also occurred. The stage was characterised by the growth of interspecific competition. Birch and pine trees started to dominate as a result of reciprocal shading by various species in the growing forest and competition for nutrients and water. *Salix acutifolia* shrubs started to die. *Cladonio-Pinetum* and *Leucobryo-Pinetum* mark the terminal stage of the succession in the area.

5   Secondary succession

Secondary succession occurs on surfaces with a preserved soil cover. It also occurs on partly damaged humic, eluvial and illuvial horizons which were blown out by wind and re-buried by aeolian sand from neighbouring areas. In both cases, sand bedrock is the initial substrate and undoubtedly influenced the course and rate of both primary and secondary successions. Such areas are easily identified in the aerial imagery for 1955, 1973 and 1996 (Fig. 4A, B and C).

The course of the secondary succession, as far as the stages and phases are concerned, is similar to the primary succession in terms of species composition.

The greatest difference is that the secondary succession occurs on fossil soil or on surfaces with blown-out sands rich in organic matter from blown-out soils. The organic matter boosts the succession rate in favourable ecological conditions. A pine coniferous forest with characteristic species may develop in such conditions over 40–50 years. Such a forest, but with only a single typical coniferous forest species, would only have begun to form in the same time if it was part of the primary succession in the desert.

A large part of Błędów Desert, especially the western part where the primary succession developed in the 1970s, has undergone a secondary forced (stimulated) succession (Fig. 4C). Single specimens played a key role in the process by introducing tree, shrub and herbaceous plant species to stabilize dry loose sand; the species chosen, mainly *Elymus arenarius, Salix arenaria, Salix acutifolia, Robinia pseudacacia* were ecologically adapted to the substratum.

In the 1970s, almost the entire western part of the desert was planted with trees. Native species (*Pinus sylvestris, Betula pendula, Alnus incana* and *A. glutinosa*) and alien species (*P. nigra, P. strobus, R. pseudacacia* and *Quercus rubra*), essential to the course of the secondary succession were introduced then.
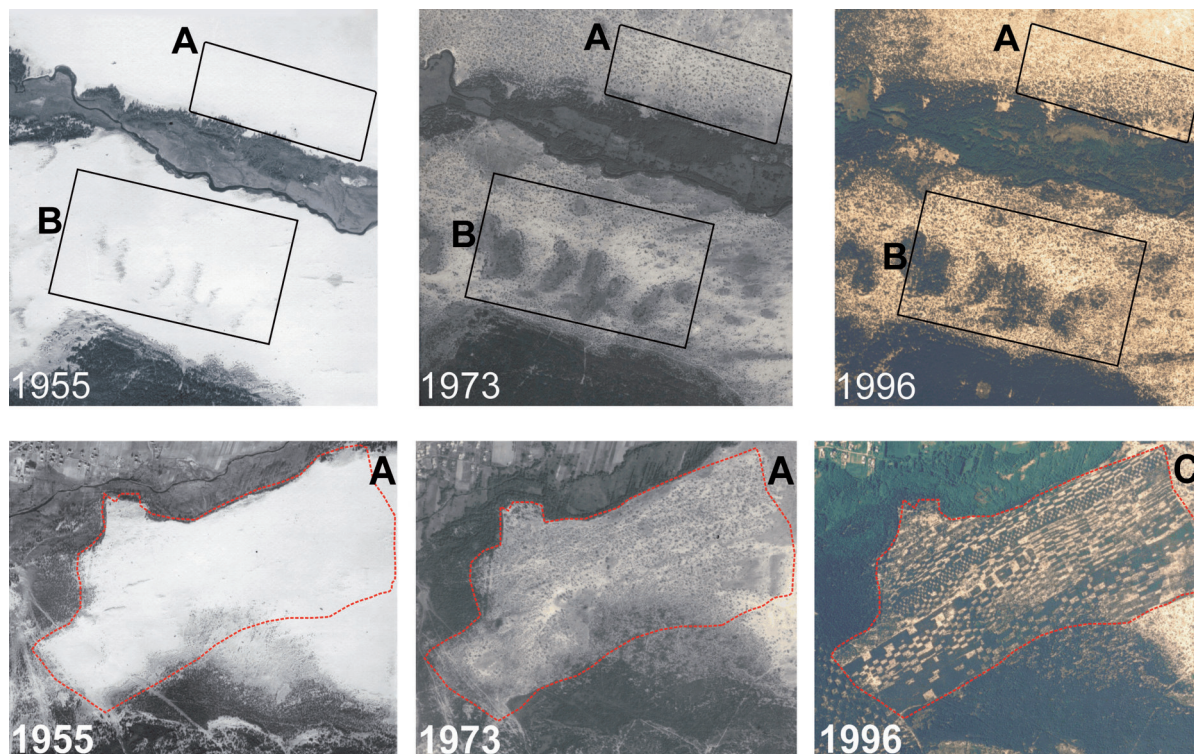

Fig. 4: The vegetation changes on selected surfaces of the Błędów Desert on aerial photographs taken in 1955, 1973 and 1996. A – area of primary succession; B – area with secondary succession on fossil soils; C – secondary stimulated succession by plantation

Artificial afforesting has decreased the range of drift sands, contributed to a slow-down of the natural succession and accelerated the anthropogenic succession. The decrease in the surface of bare sand was caused by two factors. By providing shelter from the wind, artificial planting enabled expansion in species numbers and increased the durability of the community. Secondly, the change from heliophyte to skiophyte species expanded shaded areas and changed humidity conditions. Dense artificial planting has had a negative influence on soil conditions and on the introduction of other species of the natural succession. Artificial pine forest, an example of poor monoculture not at all similar to a natural pine coniferous forest, was planted in places 30 years ago; it remains a plantation of pine.

6   Discussion

The topographic maps of 1804, 1911, 1914 and 1933 show the desert as an area mostly without vegetation. This is confirmed by PIECH (1924). Of the analysed maps, the most reliable seems to be that of 1933, which clearly distinguishes forest vegetation and damp areas.

Interpretation of aerial photographs provided very reliable information on the spatial dynamics of the vegetation cover. They also revealed forms of relief directly influenced by cryptogamous and vascular plants (RAHMONOV 2007). The correlation between relief forms and vegetation changes was confirmed in the field. It was also recognised by SZCZYPEK et al. (1994).

Primary and secondary successions in the desert are easily distinguished. The distinction is based on the state of habitats – a criterion also applied by others (CLEMENTS 1916; CONNELL and SLATYER 1977; FALIŃSKA 2003; WEST et al. 1981; WHITTAKER 1970; ELGERSMA 1998; WALKER 1999). However, it may be useful to distinguish a special type of forced secondary succession – the planting of trees to stimulate the development of a habitat and of vegetation to obtain a final vegetation community (FALIŃSKI 1986); as was termed a stimulated secondary succession by RAHMONOV (2007). In a manner similar to the way the method of distinguishing phases by comparison was used in this work (above), the method was applied by FALIŃSKA (2003) to an oak-hornbeam forest series and by FALIŃSKI (1986) to a coniferous forest series; their courses were verified by long-term observation. According to the classical succession model of CLEMENTS (1928), the mechanisms of plant competition for nutrients model of TILMAN (1990) and the facilitation model of CONNELL and SLATYER (1977), a spontaneous succession occurs in

the Błędów Desert. The way and course of succession in the investigated area is taking place according to the classical model of succession proposed by CLEMENTS (see Introduction for details).

Under aeolian conditions, poor sandy habitats may remain uninhabited for many years. Most descriptions of plant succession in such ecosystems and their course do not mention the participation of algae and cyanobacteria (e.g., COWLES 1901; OLSON 1958; CHADWICK and DALKE 1965; SYMONIDES 1979; PIOTROWSKA 1988; LICHTER 1998; HRŠAK 2004). However, they are a regular component of developing sandy ecosystems. Others have noted that algae participate in the initial stages (e.g., ZIELIŃSKA 1967; PRACH 1989; JENTSCH et al 2002; CZYLOK and RAHMONOV 2004). In the present work, a phase of the succession involving only species of algae and cyanobacteria (Tab. 2) is distinguished and their early role in the succession underlined. This phase is commonly overlooked as *Algae* and *Cyanophyta* are visible on the ground for only two or three weeks in early spring.

The bare sandy surfaces of the Błędów Desert consist mainly of rounded sand grains. The fine fraction is small. Sand surfaces covered with representatives of *Cyanophyta* and *Algae* show a reticulate character; these surfaces comprise thalluses of blue-green algae and algae that cover individual sand grains and aggregates of grains and may completely surround fine sand grains. These nets, organic membranes originating from polymers of extracellular substances (MALAM et al. 2001), are potential plant nutrients. Thus algae, secrete an extracellular jelly-like substance containing fat and saccharides, change the character of the ground and, in early spring, stabilize the sand by creating a dense enveloping net of algal filaments (RAHMONOV and PIĄTEK 2007). They initiate the primary succession.

The succession in the desert, as elsewhere, is initiated by bacteria. Unfortunately, the bacterial flora from the Błędów Desert remains unknown. The occurrence of bacteria can be assumed as algae need particular groups of bacteria for their development (SHTINA and GOLLERBAKH 1976).

Mycorrhizal fungi accelerate plant development and play a key role in ecological systems. Arbuscular mycorrhizal fungi (*Glomales, Zygomycota*) from the Błędów Desert were investigated by BŁASZKOWSKI et al. (2002) who found that *Scutellospora* are the most common fungi there, and that the most numerous species is *Scutellospora armeniaca*. All species of arbuscular mycorrhizal fungi occur in the rhizospheres of selected vascular plants growing on sandy areas.

The stage with dominating cryptogam plants can be stable for a long time if nutrient components are not added and the ground is not destroyed mechanically (Tüxen 1975; Kinder et al. 1992; Jentsch and Beyschlag 2003). The domination by cryptogams lasts from phase 1–5 in the desert and up to phase 7 in some abandoned farmlands. This clearly distinguishes the coniferous forest series of the succession from the oak-hornbeam forest series and it shows the potential properties of habitats (Faliński 1986; Cabała and Rahmonov 2004).

Aerial imagery and field investigations show that, over 60 years, fresh coniferous forest with a characteristic combination of species started growing on fossil soils in the Błędów Desert. Pine coniferous forests need more than 140 years to reach maturity on abandoned farmlands (Faliński 1986), and possibly even longer on the extremely poor soil of the desert. In the fresh coniferous forest on dune ridges, the oldest specimen is 120 years old and the soil is still at its initial stage; the community is clearly not yet a mature ecosystem. The state of the habitat and the availability of propagules when the process was initiated were significant for the length of the complete secondary succession. The desert area, after the period of complete bareness, lay within range of a biochore providing a supply of propagules; at the initiation of the succession, the neighbouring forest-meadow ecosystem was the supplier. In any case, for a given type of forest ecosystem, restoration of a typical combination of species takes less time than the creation of a proper structure and the time required to begin full functioning (Faliński 1986).

At the terminal stage, mixed birch-oak forests with pine trees, especially *Vaccinio vitis-idaea–Quercetum roburis* Oberd.57 (Ellenberg 1986), pine coniferous forests (Pott 1992) and oak-beech forests (Rode 1995) all grow on dry sandy soil poor in nutrients. For many years, the pine tree preferred by forestry formed pine forests with *Calluna vulgaris* in the undergrowth, which transferred into *Leucobryo-Pinetum*. The domination of *Leucobryo-Pinetum* or *Cladonio-Pinetum* can be seen in the Błędów area and in many other areas in Poland. Oak-beech forests with pine could develop on dry sandy soils richer in nutrients. Such forests are not rare in Poland or in Europe (Roo-Zielińska and Solon 1998).

7   Conclusions

During 1955–1996, significant changes in the vegetation cover occurred in the Błędów Desert. All were connected with the spatial dynamics of the veg-etation. After 1996, due to human interference and the spontaneous succession of willow shrubs and grass, the surface covered by vegetation increased greatly.

Old maps and aerial imagery proved to be valuable aids in the estimation of vegetation changes. They also enabled the time of formation of the forest community during the succession on poor quartz sand to be determined.

That the desert sand is poor in its variety of algal species is a direct result of the homogenous sandy substrate. The algocenosis share decreases with the increase in vascular plants and competition for ecologic niches, especially light.

The ecologic and edaphic role of a phase 0 involving *Algae* and *Cyanophyta* is significant. Algae and cyanobacteria play a major initial role in the formation of sandy ecosystems. They are essential to the stabilization of loose sand, its enrichment, moisture absorption and retention, the gathering of organic matter and the initiation of soil forming processes. Omitting this phase in similar studies may result in an incomplete understanding of the succession, its origins and different phases.

The succession rate depends on the ground; on sand surfaces inheriting the features of a parent rock, the rate is slower than on fossil soil. On naked sand, the time to complete community formation in the form of an initial pine coniferous forest, and after a full succession process, is 60 years. In areas with soil, it is less than 50 years.

The Błędów Desert is a prime example of vegetation succession on open inland sands. It is also characterized by the fact that its history and the time period of its formation are known – crucial from the point of view of ecological succession where time plays the essential role. Although it is an anthropogenic feature, the ecosystem processes in the Błędów Desert have a natural character and, thus, the results obtained have global relevance (Chadwick and Dalke 1965; Elgersma 1998; Frey and Hensen; 1995; Hršak 2004; Jeckel 1984). Anthropogenic areas of this type can make model targets for research on sandy vegetation succession.

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References

Armesto, J. J. and Pickett, S. T. A. (1986): Removal experiments to test mechanisms of plant succession in old fields. In: Vegetatio 66, 85–93. DOI: 10.1007/BF00045498

Berger-Landefeldt, U. and Sukopp, H. (1965): Zur Synökologie der Sandtrockenrasen, insbesondere der Silbergrasflur. In: Verh. Bot. Ver. Brandenburg 102, 4–98.

Błaszkowski, J.; Tadych, M. and Madej, T. (2002): Arbuscular mycorrhizal fungi (*Glomales, Zygomycota*) of the Błędowska Desert, Poland. In: Acta Societatis Botanicorum Poloniae 71 (1), 71–85.

Cabała, J. and Rahmonov, O. (2004): Cyanophyta and algae as an important component of biological crust from Pustynia Błędowska Desert (Poland). In: Polish Botanical Journal 49 (1), 93–100.

Chadwick, H. W. and Dalke, P. D. (1965): Plant succession on dune sands in Fremont County. Idaho. In: Ecology 46, 765–780. DOI: 10.2307/1934008

Clements, F. E. (1916): Plant succession and the analysis of the development of vegetation. Carnegie Institution of Washington Publication 242. Washington, DC.

–. (1928): Plant succession and indicators. New York.

Connell, J. H. and Slatyer, R. O. (1977): Mechanisms of succession in natural communities and their role in community stability and organisation. In: The American Naturalist 111, 1119–1144.

Cowles, H. C. (1901): The physiographic ecology of Chicago and vicinity. In: Botanical Gazette 31, 73–108. DOI: 10.1086/328080

Czaja, S. (2001): Mining and hydrological transformations in Upper Silesia from the fifteenth to the nineteenth century. In: The Geographical Journal 167 (1), 57–71. DOI: 10.1111/1475-4959.t01-1-00005

Czylok, A. and Rahmonov, O. (2004): The encroachment of Scot pine *Pinus sylvestris* L. on the area of former sand exploitation in the Eastern Silesian Upland. In: Brzeg, A. and Wojterska, M. (eds.): Coniferous forest vegetation – differentiation, dynamics and transformation. UAM, Seria Biologia 49. Poznań, 251–256.

Czyżewska, K. (1992): Syntaksonomia śródlądowych, pionierskich muraw napiaskowych. In: Monographiae Botanicea 74, 1–174.

del Moral, R. and Wood, D. M. (1993): Early primary succession on the volcano Mount St. Helens. In: Journal of Vegetation Science 4, 223–234. DOI: 10.2307/3236108

Drury, W. H. and Nisbet, I. C. T. (1973): Succession. In: Journal of Arnold Arboretum 54, 331–368.

Egler, F. E. (1954): Vegetation science concepts. I. Initial floristic composition – a factor in old-field vegetation development. In: Vegetatio 4, 412–417. DOI: 10.1007/BF00275587

Elgersma, A. M. (1998): Primary forest succession on poor sandy soils as related to site factors. In: Biodiversity and Conservation 7, 193–206. DOI: 10.1023/A:1008884418570

Ellenberg, H. (1986⁴): Die Vegetation Mitteleuropas mit den Alpen. Stuttgart.

Falińska, K. (2003): Alternative pathways of succession: species turnover patterns in meadows abandoned for 30 years. In: Archivum Geobotanicum 9, 1–103.

Faliński, J. B. (1986): Sukcesja roślinności na nieużytkach porolnych jako przejaw dynamiki ekosystemu wyzwolonego spod długotrwałej presji antropogenicznej. In: Wiadomości Botaniczne 30 (1), 12–50; 30 (2), 115–126.

– (2003): Long-term studies on vegetation dynamics: some notes on concepts, fundamentals and conditions. In: Community Ecology 4 (1), 107–113. DOI: 10.1556/ComEc.4.2003.1.15

Faliński, J. B.; Cieśliński, S and Czyżewska K. (1993): Atlas dynamiczno-florystyczny Rezerwatu Jelonka i przyległych obszarów. Rozmieszczenie gatunków roślin naczyniowych, mszaków i porostów na nieużytkach porolnych podlegających sukcesji wtórnej. In: Phytocoenosis 5 (3), 1-139.

Frey, W. and Hensen I. (1995): *Spergulo morisonii-Corynephoretum canescentis* (Frühlingsspark-Silbergrasflur) – Lebensstrategien von Binnendünen – und Lockersandbesiedlern. In: Feddes Repertorium 106, 533–553. DOI: 10.1002/fedr.19961060523

Fukarek, F. (1967): Fitosocjologia. PWRiL, Warszawa.

Hršak, V. (2004): Vegetation succession and soil gradients on inland sand dunes. In: Ecology Bratislava 22 (1), 24–39.

Jeckel, G. (1984): Syntaxonomische Gliederung, Verbreitung und Lebensbedingungen nordwestdeutscher Sandtrockenrasen (*Sedo-Scleranthetea*). In: Phytocoenologia 12, 9–153.

Jentsch, A. and Beyschlag, W. (2003): Vegetation ecology of dry acidic grasslands in the lowland area of central Europe. In: Flora 198, 3–25.

Jentsch, A.; Friedrich, S.; Beyschlag, W. and Nezadal, W. (2002): Significance of disturbance for seedling establishment in dry acidic grasslands dominated by *Corynephorus cancescens*. In: Phytocoenologia 32, 553–580. DOI: 10.1127/0340-269X/2002/0032-0553

Kinder, M.; Vagts, I. and Müller J. (1992): Auswirkungen der Flechtenvegetation auf die Sukzession eines Sandtrockenrasens. In: International Journal of Mycology and Lichenology 5, 67–76.

Lichter, J. (1998): Primary succession and forest development on coastal Lake Michigan sand dunes. In: Ecological Monography 68, 487–510.

Longley P. A.; Goodchild M. F.; Maguire D. J. and Rhind D. W. (2005): Geographic Information Systems and Science. Chichester.

Malam, I. O.; Le Bissonnais, Y.; Défarge, C. and Trichet, J. (2001): Role of a cyanobacterial cover on structural

stability of sandy soils in the Sahelian part of western Niger. In: Geoderma 101, 15−30. DOI: 10.1016/S0016-7061(00)00093-8

MATUSZKIEWICZ, W. (2001): Przewodnik do oznaczania zbiorowisk roślinnych Polski. PWN, Warszawa.

MIREK, Z.; PIĘKOŚ-MIRKOWA, H.; ZAJĄC, A. and ZAJĄC M. (2002): Flowering plants and pteridophytes of Poland. A checklist. Kraków.

MOLENDA, D. (1963): Mining of ores in the area of Silesian-Cracow resources till the half of 16th century. Wrocław.

OCHYRA, R. and SZMAJDA, P. (1992): Atlas rozmieszczenia geograficznego mchów w Polsce, 8, 9–14.

OLSON, J. S. (1958): Rates of succession and soil changes on southern Lake Michigan Sand dunes. In: Botanical Gazette 119, 125–170. DOI: 10.1086/335973

PEET, R. K. and CHRISTENSEN, N. L. (1980): Succession: a population process. In: Vegetatio 43, 131–140. DOI: 10.1007/BF00121025

PELKA-GOSCINIAK, J; RAHMONOV, O.; SZCZYPEK, T. and WACH, J. (2007): The influence of aeolian factor on circulation of sandy material in the sandpits of Silesian Upland (Southern Poland). In: Annales Geographicae 40 (1), 57–69.

PICKETT, S. T. A.; COLLINS, S. L. and ARMESTO, J. J. (1987): Models, mechanisms and pathways of succession. In: Botanical Review 53, 335–371. DOI: 10.1007/BF02858321

PIECH, K. (1924): Miraże w Pustyni Błędowskiej. In: Kosmos 49.

PIOTROWSKA, H. (1988): The dynamics of the dune vegetation on the Polish Baltic coast. In: Vegetatio 70, 169–175. DOI: 10.1007/BF00045762

POTT, R. (1992): Die Pflanzengesellschaften Deutschlands. Stuttgart.

PRACH, K. (1989): Primary forest succession in sand dune areas. De Dorschkamp, Research Institute for Forestry and Landscape Planning, Report 544, Wageningen.

RAHMONOV, O. (2007): Relations between vegetation and soil in initial phase of succession in sandy areas. Katowice. (in Polish)

RAHMONOV, O. and PIĄTEK, J. (2007): Sand colonization and initiation of soil development by cyanobacteria and algae. In: Ecology Bratislava 26 (1), 51–62.

RODE, M. W. (1995): Aboveground nutrient cycling and forest development on poor sandy soil. In: Plant and Soil 168/169, 337–343. DOI: 10.1007/BF00029346

ROO-ZIELIŃSKA, E. and SOLON, J. (1998): Charakterystyka geobotaniczna i analiz zasięgów borów i borów mieszanych na transektach badawczych: klimatycznym (wzdłuż 52°N, od 12° do 30°E) i „śląskim". In: Dokumentacja Geograficzna 13, 79–98.

SANTESSON, R. (1993): Het lichnes of Sweden and Norway. Lund.

SHTINA, E. A. and GOLLERBAKH, M. M. (1976): Ecology of soil algae. Moscow.

SYMONIDES, E. (1979): The structure and population dynamics of psammophytes on inland dunes. I. Population of initial stages. In: Ekologia Polska 27 (1), 3–37.

SZCZYPEK, T. and WACH, J. (1989): Accumulation phases of the Quaternary deposits in the Błędów Desert based on lithological studies. In: Quaestiones Geographicae 2, 137–145.

SZCZYPEK, T.; WACH, J. and WIKA S. (1994): Zmiany krajobrazów Pustyni Błędowskiej. Sosnowiec.

SZCZYPEK, T.; WIKA, S.; CZYLOK, A.; RAHMONOW, O. and WACH J. (2001): Pustynia Błędowska fenomen polskiego krajobrazu. Kubajak.

TILMAN, D. (1985): The resource ratio hypothesis of succession. In: American Naturalist 125, 827–852. DOI: 10.1086/284382

– (1990): Mechanisms of plant competition for nutrients: The elements of a predictive theory of competition. In: GRACE J. B. and TILMAN D. (eds.): Perspectives on plant competition. London, 117–141.

TÜXEN, R. (1960): Zur Geschichte der Sandtrockenrasen (*Festuco-Sedetalia*) im nordwestdeutschen Alt-Diluvium. In: Mitt. Flor-Soz Arbeitsgem 8, 338–341.

– (1975): Die Schrift des Bodens. Angew. Pflanzensoz. 14. Stolzenau.

WALKER, L. R. (ed.) (1999): Ecosystems of disturbed ground. Amsterdam.

WALKER L. R. and CHAPIN F. S. (1987): Interactions among processes controlling successional change. In: Oikos 50 (1), 131–135. DOI: 10.2307/3565409

WARMING, E. (1895): Plantesamfund. Grundträk af den ökologiska Plantgeografi Philipsens, Copenhagen.

WEST, D. C.; SHUGART, H. H. and BOTKIN D. B. (eds.) (1981): Forest succession. Concepts and applications. New York, Heidelberg, Berlin.

WHITTAKER, R. H. (1970): The population structure of vegetation. In: TÜXEN R. (ed.): Gesellschaftsmorphologie. Den Haag, 39–59.

ZIELIŃSKA, J. (1967): Porosty Puszczy Kampinoskiej. In: Monographiae Botanicae 24, 1–130.

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Changes in cryptogams and vascular plant species and the sequence of communities in the primary succession in the Błędów Desert

Left table

VEGETATION DEVELOPMENT PHASE	0	1	2	3	4	5	6	7	8
		INITIAL STAGE			OPTIMUM STAGE		TERMINAL STAGE		
	ALGAE and *CYANOPHYTA*	*Spergulo morisonii-Corynephoretum canescentis typicum* / *Shrubs: Salix arenaria and S. acutifolia*	*Spergulo morisonii-Corynephoretum canescentis* subass. *cladinetosum mitis*	Willow-birch shrubs with *Festuco-Koelerietum glaucae*		*Pinus sylvestris – Salix sp. – Juniperus communis – Betula pendula* - biogroups			*Cladonio-Pinetum*
		Salix arenaria Salix acutifolia / *Polytrichum piliferum*	*Festuco-Koelerietum glaucae* / Biological soil crusts Community with *P. piliferum* + lichens from genera of *Cladonia*	*Salix sp. –Pinus sylvestris - Juniperus communis – Betula pendula* - biogroups				Initial fresh pine forest	*Leucobryo-Pinetum*

ALGAE

CHLOROPHYTA
- *Cylindrocapsa sp.*
- *Klebsormidium crenulatum*
- *Stichococcus chlorelloides*
- *S. cf. fragilis*

BACILLARIOPHYCEAE
- *Pinnularia borealis*

CYANOPHYTA
- *Chroococcus varius*
- *Chroococcus minutus*
- *Chroococcus minor*
- *Gleocapsa atrata*
- *Merismopedia glauca*
- *Synoechococcus aeruginosus*

LICHENES
- *Cladonia cornuta*
- *Diploschistes muscorum*
- *Cladonia foliacea*
- *Stereocaulon condensatum*
- *Stereocaulon incrustatum*
- *Cladonia pyxidata*
- *Cladonia cervicornis ssp. verticilata*
- *Cladonia cariosa*
- *Cladonia chlorophaea*
- *Cladonia floerkeania*
- *Cladoni glauca*
- *Cladonia fimbriata*
- *Cladonia uncialis*
- *Coelocaulon aculeatum*
- *Cladonia gracilis*
- *Cladonia phyllophora*
- *Cladina mitis*
- *Cladonia subulata*
- *Cetraria islandica*
- *Cladonia furcata*
- *Cladina arbuscula*
- *Peltigera rufescens*
- *Cladonia furcata f. fissa*

BRYOPHYTA
- *Polytrichum piliferum*
- *Ceratodon purpureus*
- *Rhacomitrium canescens*
- *Brachythecium albicans*
- *Polytrichum juniperinum*
- *Bryum capillare*
- *Pohlia nutans*
- *Pleurozium schreberi*
- *Hylocomium splendens*
- *Hypnum cupressiforme*
- *Dicranum polysetum*
- *Dicranum scoparium*
- *Climacium dendroides*

Right table

VEGETATION DEVELOPMENT PHASE	0	1	2	3	4	5	6	7	8
		INITIAL STAGE			OPTIMAL STAGE		TERMINAL STAGE		
	ALGAE and *CYANOPHYTA*	*Spergulo morisonii-Corynephoretum canescentis typicum*	*Spergulo morisonii-Corynephoretum canescentis* subass. *cladinetosum mitis* / Shrubs: *Salix arenaria and S. acutifolia*	Willow-birch shrubs with *Festuco-Koelerietum glaucae*		*Pinus sylvestris – Salix sp. – Juniperus communis – Betula pendula* - biogroups			*Cladonio-Pinetum*
		Salix arenaria Salix acutifolia / *Polytrichum piliferum*	*Festuco-Koelerietum glaucae* / Biological soil crusts Community with *P. piliferum* + lichens from genera of *Cladonia*		*Salix sp. –Pinus sylvestris – Juniperus communis – Betula pendula* - biogroups			Initial fresh pine forest	*Leucobryo-Pinetum*

WOODY SPECIES:

(Tree layer - a, Shrub - b, Herb layer - c)
- *Betula pendula* ROTH — b, c
- *Juniperus communis* L. — a, b, c
- *Pinus sylvestris* L. — b, c
- *Populus tremula* L. — b, c
- *Quercus robur* L. — a, b, c
- *Robinia pseudacacia* L. — b, c
- *Salix acutifolia* WILLD. — b
- *Salix arenaria* L. — b
- *Sorbus aucuparia* L. em. HEDL. — b

EARLY SUCCESSION SPECIES
psammophilous species
- *Oenothera biennis* L. s. s.
- *Jasione montana* L.
- *Elymus arenarius* L.
- *Echium vulgare* L.
- *Carex hirta* L.
- *Herniaria glabra* L.
- *Dianthus deltoides* L.
- *Dianthus carthusianorum* L.
- *Armeria maritima* (MILL.) WILLD. subsp. *elongata* (HOFFM.)BONNIER
- *Arenaria serpyllifolia* L.
- *Thymus serpyllum* L. em. FR.
- *Thymus pulegioides* L.
- *Trifolium arvense* L.
- *Sedum acre* L.
- *Artemisia absinthium* L.
- *Scleranthus perennis* L.
- *Scleranthus annuus* L.
- *Artemisia campestris* L.
- *Cerastium arvense* L
- *Cerastium semidecandrum* L
- *Hypericum perforatum* L.
- *Euphorbia cyparissias* L.
- *Euphrasia rostkoviana* HAYNE
- *Euphrasia stricta* D. WOLFF ex J. F. LEHM.
- *Festuca psammophila* (HACK. ex CELAK.) FRITSCH
- *Epipactis atrorubens* (HOFFM.) BESSER
- *Koeleria glauca* (SPRENG.) DC.
- *Hieracium pilosella* L.
- *Rumex acetosella* L.
- *Festuca ovina* L.
- *Corynephorus canescens* (L.) P. BEAUV.
- *Cardaminopsis arenosa* (L.) HAYEK
- *Carlina acaulis* L.

LATE SUCCESSION SPECIES
forest species
- *Chimaphila umbellata* (L.) W. P. C. BARTON
- *Deschampsia flexuosa* (L.) TRIN.
- *Orthilia secunda* (L.) HOUSE
- *Vaccinium vitis-idaea* L.
- *Vaccinium myrtillus* L.
- *Hieracium lachenalii* C. C. GMEL.
- *Epipactis helleborine* (L.) CRANTZ
- *Chamaecytisus ratisbonensis* (SCHAEFF.) ROTHM.
- *Hieracium umbellatum* L.
- *Pyrola chlorantha* SW.
- *Pyrola minor* L.
- *Calluna vulgaris* (L.) HULL
- *Fragaria vesca* L.

A - - - - - the species encroachment in the initial stage of succession

B ——— optimum occurrences of species during the succession

C ········· the species withdrawal in terminal stage of succession.