VEGETATION SUCCESSION AND SOIL GRADIENTS ON INLAND SAND DUNES

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Abstract

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A part of the sand dune area with the best-preserved pioneer sand vegetation in the vicinity of the town of Đurđevac in northern Croatia was declared a Botanical Reservation in 1963. Since then natural succession and other vegetation types replaced the pioneer sand vegetation. Vegetation succession was studied using the space-for-time substitution approach. The environmental features related to the succession process were also studied. The co-structure among the succession stages and some soil features were established by constrained ordination (Co-Inertia Analysis). Organic matter and nitrogen contents showed the strongest relation with the vegetation structure. These two soil properties are assumed to be the most important driving forces for vegetation succession on sand. Therefore, all measures for slowing down or halting vegetation succession with the aim of conservation or recovering the pioneer sand vegetation need to be focused on reducing the organic matter and nitrogen in the soil.

Key words: co-inertia analysis, constrained ordination, direct gradient analysis, indicator species analysis, *Koelerio-Corynephoretea*, sand vegetation

Abbreviations: Bold letters in Appendix 1 are abbreviations of plant species names in ordination graphs, CA = Correspondence Analysis, CIA = Co-Inertia Analysis, ISA = Indicator Species Analysis, PCA = Principal ComponentAanalysis; TWINSPAN = Two Way INdicator SPecies ANalysis

Introduction

In Croatia, sand dunes are rare and cover only a small area (Radović, 2000). Consequently, the related plant species and vegetation types are limited to a small number of localities. The largest areas of sand dunes are found in the Drava river valley in northern Croatia. The Drava river marks the border with neighbouring Hungary, and its right bank is situated in Croatia in the greatest part of its course. The sand dune area in northern Croatia consists of several unconnected areas whose total area is approximately 450 ha. These sand dunes originate from the drifts of the river Drava in the Tertiary Age when this was the mouth of the river flowing into the Pannonian Sea (Soklić, 1943). When the sea drew back from this area, the winds turned the deposited sand dunes into shifting sand dunes. The sand is dominated by silicates and originates in the central Alps (Kučan, 1913/14; Martinović et al., 1986).

By the end of the 19th century the major part of the sands was bare shifting sand dunes. These shifting sand dunes caused damage in the cultivated areas nearby. Therefore, afforestation was started in 1899, reaching its peak intensity in the period from 1924 to 1930 (Martinović et al., 1986). These formerly mobile dunes were fixed by afforestation. At present the majority of those areas are covered by forests dominated by Austrian pine (*Pinus nigra*) at some places and by Locust-tree (*Robinia pseudacacia*) at others. Subsequently, the area with shifting sand and pioneer sand vegetation decreased.

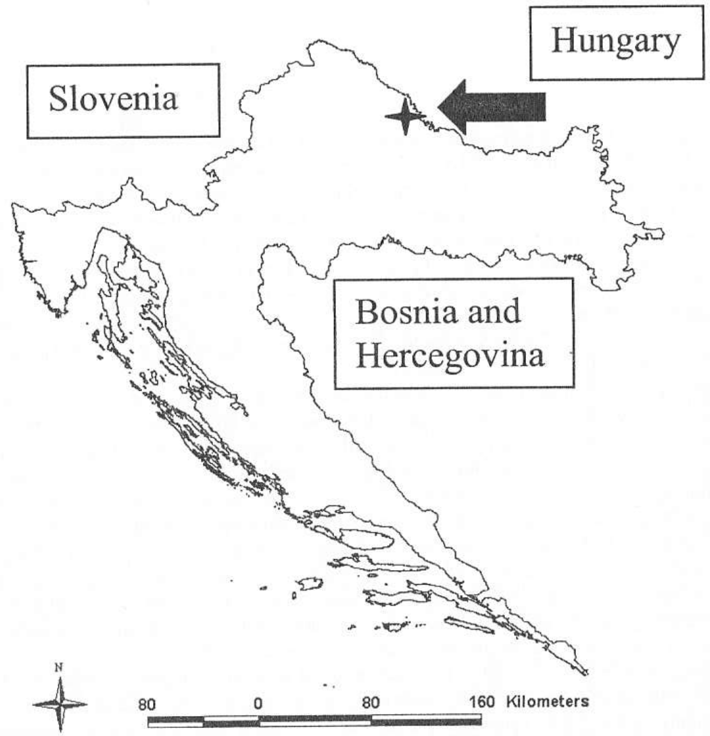

Fig. 1. Location of the Đurđevac Sands Botanical Reservation in Croatia.

In the 1960s only a small area with preserved pioneer sand vegetation remained in the vicinity of the city of Đurđevac. In 1963 it was declared a Botanical Reservation with the intention of preserving the remaining part of the sand dune area. This area was then partly shifting sands, partly covered only by pioneer sand vegetation. Before it was declared a Reservation this fragment of the sand dunes area was used as a common pastureland by the local farming community. Grazing influenced the vegetation by removing the plant biomass. Unfortunately, since at the moment of its designation no scrutinised botanical research was carried out, any documented comparative study with the current situation is impossible. Since 1963 this area was left to rest without any intensive activities being performed.

The research was carried out and aimed to establish patterns of the vegetation succession and the environmental gradients underlying these processes. The insights gained by this research should represent the basis for prescribing the measures that would have to be undertaken in order to stop the succession process, and preserve or even attempt restoration of the pioneer sand vegetation.

Methods

Study area

The Đurđevac Sands Botanical Reservation is situated about 5 km east of the town of Đurđevac in northern Croatia (46^0 01' N, 17^0 05' E) and covers 19.5 ha. The climate in that part of Croatia can be described by the data from the closest meteorological station of Koprivnica which is 20 km away from the Reservation. According to the Köppen classification it is Cfwbx", and according to the Thornthwaite classification it is humid (P/E = 88). Mean annual temperature is 10.1°C, and mean annual precipitation sum 950 mm.

Nowadays, the vegetation forms a mosaic of patches with different types of grassy and shrub-like vegetation. The microreliefs are geomorphologically typical sand dunes 2-4 m high with a mosaic-like interplay of smaller patches dominated by different grasses or shrubs. According to the local forestry office the areas covered by pioneer sand vegetation are considerably reduced. This opinion is supported by old photographs taken at the beginning of 20th century (Šandor, 1911; Soklić, 1943).

Soklić (1943) studied the pioneer sand vegetation in the entire area of the sand dunes in the region. Already at that time, bare sand dunes were present in small patches only. The greatest part was covered by fixed dunes, but was covered by pioneer grassy sand vegetation and other vegetation types. Soklić used Braun-Blanquet approach (Braun-Blanquet, 1928) and phytosociologically characterised it as a *Corynephoreto-Festucetum vaginatae croaticum*. He gave this name because he believed the association was somewhat different from similar vegetation described in Hungary under the names *Festucetum vaginatae* and *Festuceto-Corynephoretum* (Aszod, 1936). Soklić (1943) also distinguished three subassociations: subass. *initiale*, subass. *typicum* and subass. *sterile*, and divided each into several facies depending on the dominant species. This is unsatisfactory and complicated, but can be explained by the general mosaic character of the dune vegetation with many patches of different dominating species. Many of these patches do not contain a full floristic-sociological assemblage because they do not reach the minimal area size (Van der Maarel et al., 1985).

It is interesting to note that this area is the meeting point of sand plant species belonging to the Central European and the Pannonian flora. This is the result of the geographic position of the area, which is the western rim of the Pannonian plain. Thus, Pannonian plants such as *Festuca vaginata*, *Linaria angustissima*, pontic-sarmatic species such as *Hieracium echioides*, *Anthemis ruthenica*, *Potentilla arenaria*, the Baltic plant *Thymus serpyllum* subsp. *serpyllum*, and the subatlantic plant *Corynephorus canescens* can be found together here.

Vegetation sampling

Vegetation succession was researched using one of the indirect methods – space-for-time substitution (Pickett, 1989). This approach is accepted as an alternative to the long-term studies in the research of the vegetation succession (Dierschke, 1994; Glavac, 1996). In the Botanical Reservation area, 22 sites were selected by preferential sampling. Chosen were the sites considered as members of the succession chronosequence according to the presumed underlying gradient responsible for the vegetation succession from sand pioneer to shrub vegetation.

The size of the sample plots (relevés) was 20 m². Besides, on one sand dune a small closed transect was studied by means of 1x7 m plots dominated by species which were assumed to be indicators of the underlying gradient (sites 7a-c). Together they make up a 21 m² area similarly to the other sampling sites, but were recorded in three parts as they were assumed to represent the underlying environmental gradient on a small scale. The species abundances were assigned by combined cover/abundance estimation according to the expanded scale (Barkman et al., 1964). The estimated cover/abundance values were then transformed into the ordinal scale according to Van der Maarel (1979).

Nomenclature of the plant species follows Nikolić (ed.) (1994, 1997, 2000)

Soil sampling and analyses

On all sites soil samples were collected from a depth of 0-10 cm. All samples were a mixture of 5 subsamples to prevent small-scale soil variability. Soil samples were air-dried and then analysed.

The measurements included:

pH – electrometrically in redistilled water and 0.1 M KCl in a suspension 1:2.5
organic matter according to Kotzmann (Steubing, 1965)
total nitrogen according to Kjeldahl-Foerster (Steubing, 1965)
total exchangeable bases (TEB) and hydrolytic acidity (HyA) (Schlichting & Blume 1965)

Data processing

The environmental and vegetation data sets were treated separately at first. The environmental data set was first treated via Principal Component Analysis (PCA) performed on a correlation matrix (standardised data) (Okland, 1990; Jongman et al., 1995). The vegetation data set was treated via Correspondence Analysis (CA). The species that occurred only in one record were not considered in the data processing and their names are not in bold type in Appendix 1. The relationships between environmental and vegetation data were treated via Co-Inertia Analysis (CIA) (Mercier et al., 1992; Doledec, Chessel, 1994). This analysis allows the simultaneous ordination of two data matrices sharing the same set of rows. It calculates co-inertia axes maximising the covariance of the factorial scores generated in the separate ordinations of the two data sets (in this study a PCA of the environmental data set, and a CA of the vegetation data set). CIA provides an ordination of the common structure of the two data sets that maximises simultaneously the variance of the factorial scores from separate tables, and their correlation. CIA generates factorial scores, which can be used for graphical displays as in standard ordination graphs. This analysis was chosen since it enables the joint analysis of tables having similar (even low) as well as different numbers of environmental variables, species and samples, avoiding the arch effect in Canonical Correspondence Analysis (CCA), and the instability of Detrended Canonical Correspondence Analysis (DCCA) (Tausch et al., 1995; Oksanen, Minchin, 1997).

Separate PCA, CA and CIA analyses and resulting graphics were made using ADE-4 for Windows software (Thioulouse et al., 1997; Chessel et al., 1998). Vegetation table (Appendix 1) was arranged according to the results of the TWINSPAN (Hill, 1979; Gauch, Whittaker, 1981). To determine which species are most strongly separated among the vegetation types Indicator Species Analysis was performed followed by Monte-Carlo significance test with 1000 random permutations (Dufrene, Legendre, 1997). Groups of sampling sites were defined by cluster analysis performed by Ward's method of linkage and Sorensen distance measure. Groups were considered for the following Indicator Species Analysis (ISA) at four cluster levels because on this level all clusters had at least two members, which is a condition for successful ISA. As indicators were considered species whose relative abundance in one cluster of sites was over 50% at probability level $p < 0.05$. TWINSPAN, cluster and Indicator Species Analysis were performed using PC-Ord 4.14 software (McCune, Mefford, 1999). T-tests were performed using Statistica for Windows software (Statsoft, 1998).

Results

Separate analyses

The environmental data set was analysed via correlation matrix PCA. According to the eigenvalue analysis, the first two eigenvalues account for 83% of the data variability and therefore are sufficient to demonstrate the data set structure (Fig.2A).

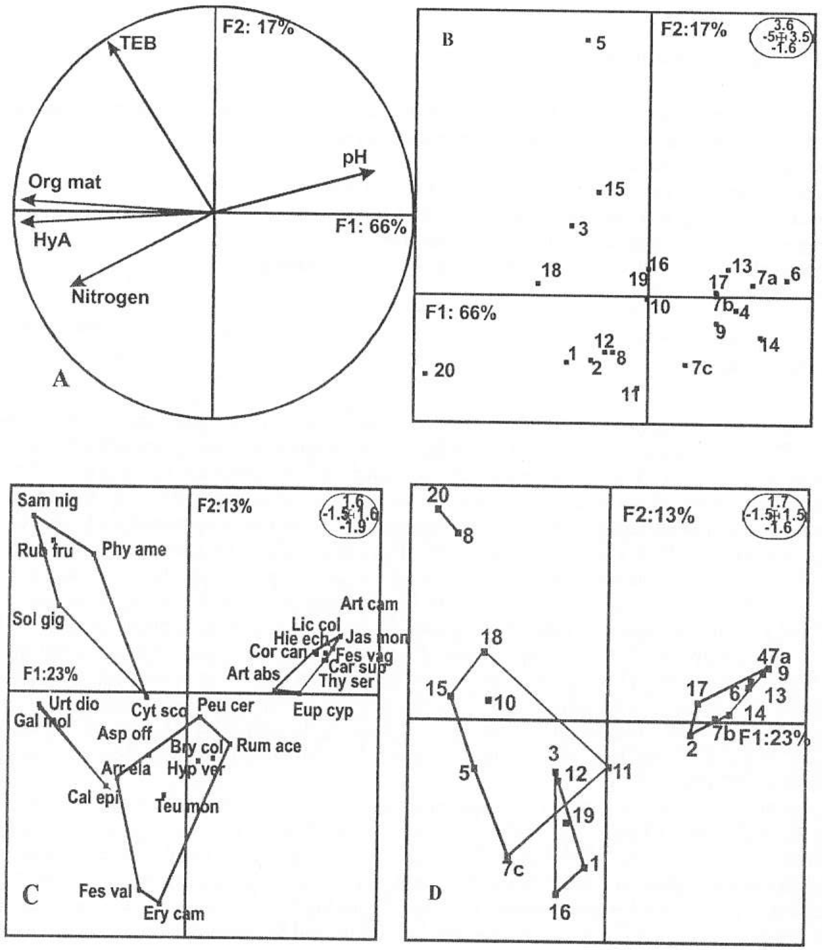

Fig. 2. PCA ordination of the 22 sampling sites by 5 environmental variables and CA ordination of the 22 sampling sites and 27 plant species and superimposed cluster analysis. A – correlation circle of environmental variables with the two first PCA ordination axes (F1 and F2 with percentage of explained variance); B – first factorial plane of PCA ordination of sample sites; C – first factorial plane of CA ordination of species; D – first factorial plane of CA ordination of sample sites.

The correlation circle (Fig.2A) demonstrates a high negative correlation of organic matter, hydrolytic acidity and soil nitrogen, and a high positive correlation of pH-values with the first ordination axis. The total exchangeable bases (TEB) are highly correlated with second ordination axis. The factorial plane F1 x F2 (Fig.2B) arranges sampling sites according to chemical soil properties. On the positive end of F1 are the sites with the lowest contents of organic matter and nitrogen (sites 4, 6, 7a, 7b, 9, 13, 14, 17). On the opposite end of the F1 axis lies site 20 with the largest organic matter and soil nitrogen contents. Site 5 is ordinated high on axis 2 due to the highest contents of total exchangeable bases.

The vegetation data set has been analysed via Correspondence Analysis and superimposed Cluster Analysis. According to the eigenvalue analysis first four eigenvalues account for 57% of the data variability. The biplot of sites and species has been split into Figures 2C and 2D. Fig. 2C demonstrate the species ordination along the floristic composition gradient. Groups of species are defined as a result of cluster analysis as belonging to same cluster. Fig 2D demonstrates the sites ordination along the floristic composition gradient with superimposed clusters achieved by cluster analysis. On the right end of the ordination axis 1 are the sites of pioneer sand vegetation (2, 4, 6, 7a, 7b, 9, 13, 14, 17). The following species were established as the indicator species of this type of vegetation *Corynephorus canescens*, *Festuca vaginata*, *Euphorbia cyparissias*, and *Lichenes*. The next cluster consists of sites 1, 3, 12, 16, 19 with *Rumex acetosella* and *Teucrium montanum* as indicator species. These sites were dominated by or contain a considerable abundance of *Cytisus scoparius*. This species is not established as indicator species in indicator species analysis because it occurred at some of the sites belonging to other clusters and therefore has no appropriate significance level. In the middle are the sites dominated by *Calamagrostis epigejos* as indicator species only (5, 7c, 10, 11, 15, 18). These sites are transitional towards sites 8 and 20 which are fully dominated by the shrub-like species established as indicators *Rubus fruticosus*, *Sambucus nigra*, *Solidago gigantea*.

Co-Inertia Analysis

The co-structure between the environmental and the vegetation data sets revealed by CIA was very highly significant, as confirmed by a Monte-Carlo permutation test ($p < 0.001$).

According to the eigenvalue analysis the first two ordination axes explained 85.0% and 10.6% of the total inertia. This means that the F1 x F2 factorial plain visualises the co-structure of the two data sets very well.

The relationship between the principal axes resulting from separate analyses and co-inertia analysis, i.e. each table structure and their co-structure, is visualised in Fig.3A and Fig.3B. Both axes resulting from the environmental data set ordination are negatively correlated against the co-inertia axes. From the vegetation data set ordination, the first ordination axis is negatively correlated with the first co-inertia axis.

T a b l e 1. Summary of co-inertia statistics (Covaria – maximised covariance projected on co-inertia axes; Varian1 and Varian2 – inertia projected on co-inertia axes; Correla. – correlation of two coordinate systems for co-inertia axes 1 and 2; INER1 and INER2 maximal inertia resulting from separate analyses (first and second eigenvalues)

Num	Covaria.	Varian1	Varian2	Correla.	INER1	INER2
1	1.342	3.292	0.7202	0.8713	3.302	0.7745
2	0.4705	0.8464	0.3601	0.8522	0.8691	0.4499

Table 1 gives a summary of the co-inertia analysis statistics. The Iner 1 column represents the maximal inertia of the environmental data set separate analysis and the Iner 2 column represents the maximal inertia of the vegetation data set separate analysis. The Varian 1 column represents the inertia of the environmental data set projected on the co-inertia axes. The values of the projected inertia are close to the values of the inertia of separate analyses. The Correl. column represents the correlation between the F1 and F2 co-inertia axes of two data sets. The correlation coefficients (R = 0.87 for F1 axis, and R = 0.85 for F2 axis) show that the two co-ordinate systems are highly correlated.

The link between species and environmental variables, i.e. correlation of the two data site scores, is represented in Fig. 3C. Each sample site is represented by an arrow. The beginning of the arrow marks the score of the site according to the environmental table ordination and arrowhead indicates the score according to the vegetation table ordination. The two structures have been found similar in global terms. However, the quite long arrows of some sites (2, 3, 7c, 8, 15, 20) indicate low relationships between environmental and vegetation features. The sites with the pioneer sand vegetation (4, 6, 7a, 7b, 9, 13, 14) show an average higher relationship between vegetation and environmental features (an exception is site 17).

The canonical weight of each environmental variable is represented in Fig. 4A. The first co-inertia axis is highly correlated with the organic matter; hence it represents an organic matter gradient. The second axis represents the total exchangeable bases gradient. Figure 4B represents ordination of sites along the co-inertia axes from the environmental viewpoint. A positive correlation to the organic matter gradient, which is represented by first ordination axis, was found in the sites (sites 5, 15, 18, 20) where shrub-like species such as *Sambucus nigra*, *Rubus fruticosus*, *Cytisus scoparius*, and sometimes *Calamagrostis epigejos* and *Solidago gigantea* (site 3) (Appendix 1) are abundant. An intermediate position in the organic matter gradient is found at sites characterised by the dominance of *Calamagrostis epigejos* (sites 1, 2, 7c, 8, 10, 11, 12, 16, 19) as well (Appendix 1). A negative correlation to the soil organic matter content (ordinated on the negative side of the first axis) was established at the sites dominated by pioneer sand vegetation species such as *Corynephorus*

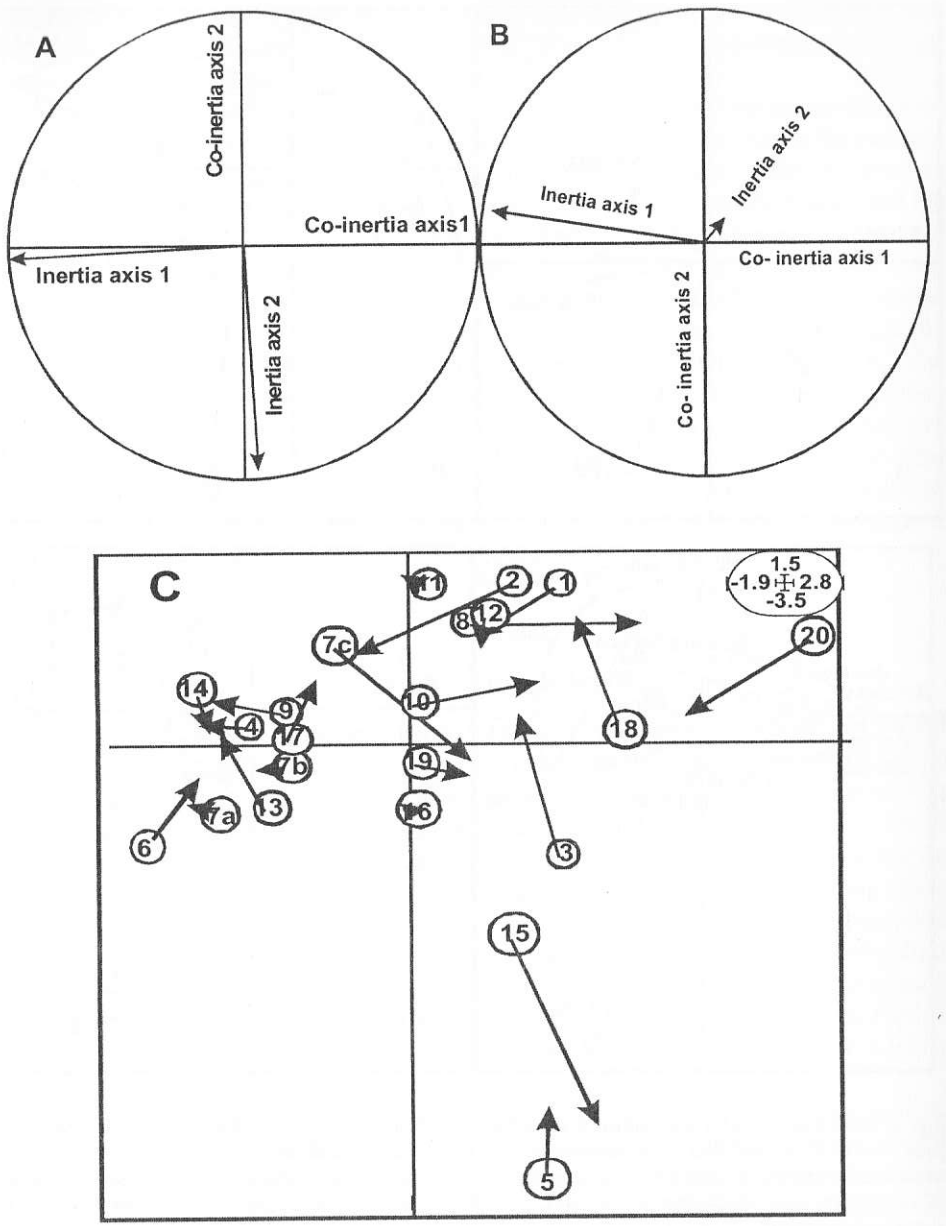

Fig. 3. A – B – projection of the axes resulting from each separate analysis (A – environmental table; B – vegetation table); C – Standardised Co-Inertia scores of the environmental and vegetation data sets projected onto F1 x F2 factorial map. Arrows link environmental scores (beginning of the arrow) to vegetation ones (arrowhead). The shorter the arrow is the better correlation between the two structures is.

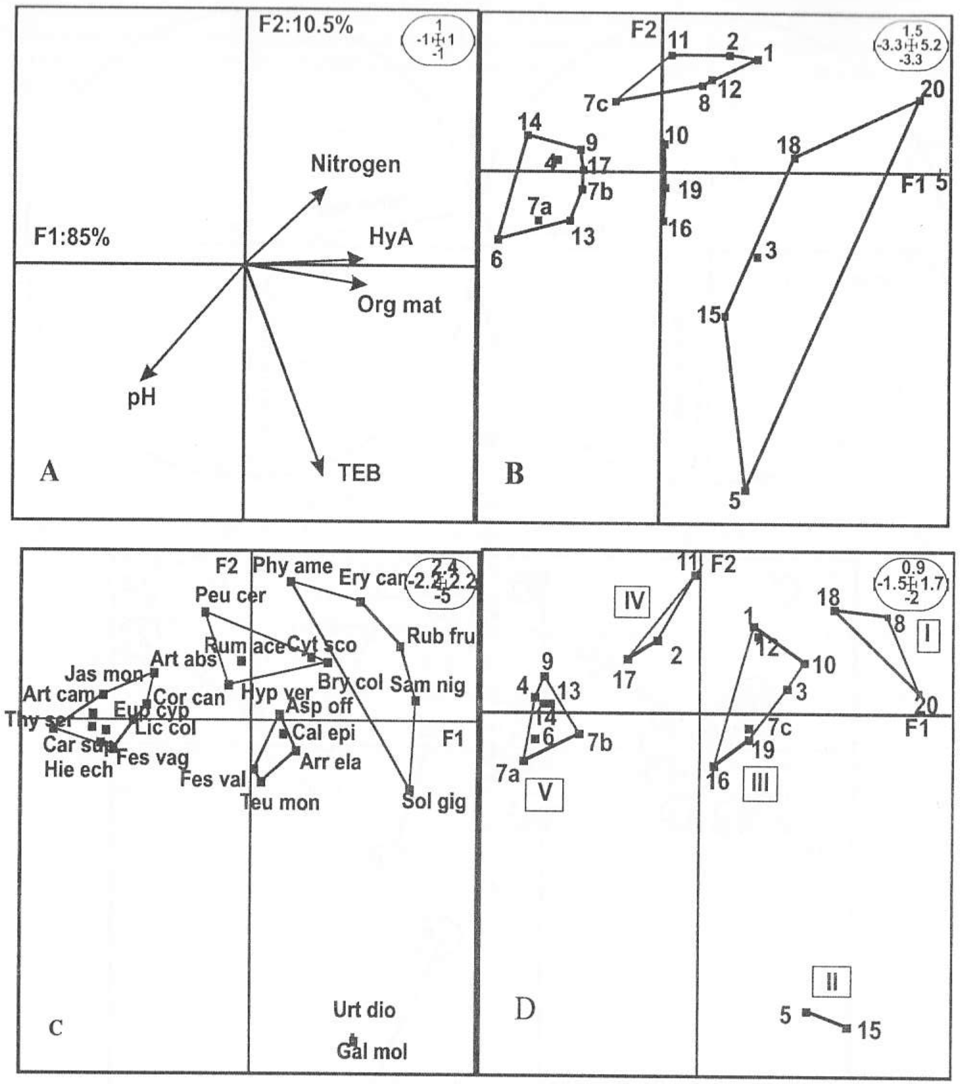

Fig. 4. Results of CIA of 5 environmental variables and 27 plant species from 22 sampling sites. A and B – projection of 22 sample sites by 5 components array via Co-Inertia analysis (A – weights of environmental variables; B – ordination according to environmental variables); C and D – projection of the 22 sample sites by 27 components array via Co-Inertia analysis (C – weights of plant species; D – ordination of sites according to species composition).

canescens, *Festuca vaginata*, as well as at sites with a high abundance of *Lichenes* and *Bryophyta*. A biplot of partially maximised projected inertia, since environmental typology is also used, has been split into Figs 4C and 4D.

Figure 4C shows the co-inertia weights of plant species and Fig.4D represents the corresponding first factorial plane. The resulting ordination of sites is connected to the environmental typology. The sites are then placed at the weighted average of the species they present. These scores maximise the sum of the squared covariance of the species and the environmental variables. This ordination graph has 5 groups of sites. Group I is made up of sites of a scrub vegetation type dominated by shrub species such as *Rubus fruticosus*, *Sambucus nigra*, and the ruderal species *Solidago gigantea*. Group II (sites 5 and 15) contains, the ruderal species *Urtica dioica*, *Galium mollugo* in addition to the dominant species *Calamagrostis epigejos* and, all of which appear on base rich soils. Group III (sites 1, 3, 7c, 10, 12, 16, 19) encompasses the sites dominated by *Calamagrostis epigejos* although they also include *Cytisus scoparius* shrubs. Group IV (sites 2, 11, 17) consists of sites with *Rumex acetosella* and *Cytisus scoparius*, as well as *Calamagrostis epigejos*. Group V (sites 4, 6, 7a, 7b, 9, 13, 14) comprises sites dominated by pioneer sand species *Festuca vaginata*, *Corynephorus canescens*, *Artemisia campestris*, *Thymus serpyllum* with a low soil organic matter content.

Discussion

In the past, shifting dunes were fixed by the planting of Scots pine (*Pinus sylvestris*), Austrian pine (*Pinus nigra*) and shrubs such as English broom (*Cytisus scoparius*). Attempts were made to protect only smaller areas with shifting dunes or pioneer vegetation (Van Rheenen et al., 1995). Similar attempts were made in the sand dune area of northern Croatia in the vicinity of the town of Đurđevac (Martinović et al., 1986). The sands allow the spontaneous development of pioneer sand vegetation, which also fixes the shifting sands. In western and central parts of Europe such pioneer vegetation is dominated by *Corynephorus canescens* and *Spergula morisonii* (Van Rheenen et al., 1995; Grau et al., 1996; Schwabe et al., 2000). On the Đurđevac Sands pioneer vegetation is dominated by *Corynephorus canescens* which, unlike in Central Europe, is joined by the Pannonian grass species *Festuca vaginata*, and some other Pannonian plants such as *Viola kitaibeliana*, and *Linaria angustissima* (Loisel.) Borbás (not recorded in the sample plots).

In further succession, pioneer sand dune vegetation is usually replaced by grassland and subsequently by shrub (Van Rheenen et al., 1995; Berendse et al., 1998) and forest vegetation (Van der Maarel, 1985; Gallé et al., 1998). Thus the Đurđevac Sands area developed a grassy successional stage dominated by *Calamagrostis epigejos* at some patches, and shrub stage at others. The shrub stage is dominated by different shrub species at different places. Thus some patches are dominated by *Cytisus scoparius*, others by by *Rubus fruticosus*, and others by *Sambucus nigra*. It is particularly interesting to observe the occurrence of ruderal species such as *Urtica dioica*, *Solidago gigantea*, *Sambucus nigra* in some places, as well as neophytes *Phytolacca americana*, *Conyza canadensis* and *Oenothera biennis* in other places (not in the sample sites, but in the Reservation area). Also in other countries of Europe sand habitats have ruderalised as indicated by the settlement of ruderal species such as *Conyza canadensis*, *Oenothera* sp. div. and others (Schwabe et al., 2000).

In several studies an increase of soil organic matter and total nitrogen was established in subsequent succession stages (Van der Maarel et al., 1985; Berendse, 1990; Berendse, Elberse, 1990; Olff et al., 1993; Berendse et al., 1998) and is also linked to the ruderalisation of sands (Rohde, 1994; Quinger, Meyer, 1995; Van Rheenen et al., 1995; Leuschner, Gerlach, 2000). Thus it has been established that the organic matter level can increase 2-16 times, while total nitrogen can go up even 13 times in succession stages and ruderalised sand habitats compared to the initial succession stage (Van Rheenen et al., 1995; De Kovel et al., 2000; Schwabe et al., 2000). Likewise, on average, 2.2 times more organic matter (3.7 vs. 1.7 g/100g, t-test $p < 0.01$) and even 13 times more total soil nitrogen (0.46 vs. 0.035 mg/100g, t-test $p < 0.01$), was found on the Đurđevac Sands in the successional stages compared to the pioneer sand vegetation. The total amount of nitrogen is important only as a source of mineral nitrogen which is only available for higher plants. Mineral nitrogen is produced by mineralisation of organic matter. The nitrogen mineralisation rate in sand ecosystems is usually low (Berendse et al., 1998), but is usually 7-8 times higher in older succession stages compared to the pioneer stages (Berendse, 1990; Gerlach, 1993; Gerlach et al., 1994; Berendse et al, 1998). Apart from the mineralisation of organic matter, the nitrogen level also increases from the intake from polluted atmosphere. In western and central parts of Europe in nutrient poor ecosystems the nitrogen intake from the atmosphere is approximately of the same quantity (Emmer, Sevink, 1994; Rode, 1995) or even larger as the nitrogen mineralisation rate (Van Oene et al., 1999). In this way large amounts of nitrogen are accumulated in the sand ecosystems, thus facilitating the settlement of ruderal species and facilitating an increase in succession rate to shrub and wood communities (Rohde, 1994; Quinger, Meyer, 1995; Van Rheenen et al., 1995; Leuschner, Gerlach, 2000). As yet we do not have reliable local data of the nitrogen intake from air pollution in the Đurđevac Sands area.

Another source of nitrogen can also be nitrogen fixing (Leuschner, Gerlach, 2000). In the Reservation area English broom shrubs (*Cytisus scoparius*) occur in great abundance. This species is able to fix nitrogen and may raise soil fertility (Fogarty, Facelli, 1999).

It is commonly accepted that the accumulation of nutrients in the pioneer vegetation enables further succession. As stated by Berendse (1990), the accumulation of organic matter and nitrogen in an ecosystem is probably one of the main driving forces in determining the rate of succession. The results of constrained ordination in the case of the Đurđevac Sands also show the relationship between vegetation succession stages, which substitute and suppress pioneer sand vegetation, with the organic matter and nitrogen contents in soil. The connection with the pH values is much weaker, although the pH on the Đurđevac Sands is statistically significantly lower in the successional stages than in the pioneer vegetation (pH 4.7 vs. pH 5.1, t-test; $p < 0.05$). The successions on the acid soils, as found at the Đurđevac Sands Reservation, usually show minimal changes in pH values (Leuschner, Gerlach, 2000). On neutral soils the decline can be over two pH units (Berendse et al., 1998).

Therefore, it can be assumed that the accumulation of soil organic matter and nutrients, particularly nitrogen, is the chief factor that encourages the succession process and that jeopardises the survival of pioneer sand vegetation. Hence, all measures necessary to preserve pioneer vegetation should be directed primarily towards reducing soil organic matter and nitrogen level. The most practical solution is to return the area to some form of grazing regime. Grazing might have the effect of adding nitrogen in the short run, but would reduce vegetation cover and soil organic matter and preserve pioneer sand vegetation. All this, if carefully managed, could enable the conservation of the dunes in the long run.

Translated by the author

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Hršak V.: **Vegetačná sukcesia a pôdne stupne na vnútrozemských pieskových dunách.**

V roku 1963 bola časť pieskových dún s najlepšie zachovanou vegetáciou v okolí mesta Durdevac v severnom Chorvátsku vyhlásená za Botanickú rezerváciu. Odvtedy prírodná sukcesia a ďalšie vegetačné typy nahradili pioniersku pieskovú vegetáciu. Vegetačnú sukcesiu sme skúmali priestorovo-časovým prístupom. Skúmali sme i environmentálne charakteristiky vo vzťahu k procesu sukcesie. Spoločnú štruktúru medzi sukcesnými štádiami a niektorými pôdnymi vlastnosťami sme stanovili co-inertnou analýzou. Obsah organickej hmoty a dusíka javí najsilnejší vzťah so štruktúrou vegetácie. Predpokladáme, že tieto dve pôdne vlastnosti sú najdôležitejšími hnacími silami vegetačnej sukcesie na piesku. Všetky opatrenia na zníženie sukcesií s cieľom zachovať alebo prinavrátiť pioniersku vegetáciu na piesok by sa preto mali sústrediť na redukciu organickej hmoty a dusíka v pôde.

Appendix 1. Vegetation table arranged according results of TWINSPAN (bold letters are the abbreviations of the species names in the ordination graphs; species without bold letters were skipped in the ordination analyses; cover/abundance values are according to Barkman et al. (1964))

Species	6	7a	14	4	9	13	17	2	7b	11	12	1	3	16	19	7c	10	18	8	20	5	15
Thymus serpyllum	1	-	1	r	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bromus tectorum	r	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alyssum gmelini	r	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euphorbia cyparissias	1	-	2m	r	+	r	r	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
Carex supina	-	-	r	-	-	r	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Artemisia campestris	1	-	+	2a	2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Jasione montana	-	-	1	r	1	r	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hieracium echioides	1	-	r	+	-	+	2a	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carex hirta	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anthemis ruthenica	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lichenes coll.	2a	2	-	4	3	2a	2b	2m	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Corynephorus canescens	2b	-	-	2a	3	2m	2b	2m	-	r	-	-	-	-	-	-	-	-	-	-	-	-
Festuca vaginata	3	5	2a	2m	r	5	r	2m	5	-	-	-	-	-	-	-	-	-	-	-	-	-
Bromus hordeaceus	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Artemisia absinthium	-	-	r	-	-	r	r	-	-	r	-	-	-	-	-	-	-	-	-	-	-	-
Arabis glabra	-	-	-	-	-	-	-	-	-	r	-	-	-	-	-	-	-	-	-	-	-	-
Elymus repens	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rumex acetosella	-	-	1	2m	2m	2m	r	2a	1	3	2m	4	2m	-	2b	-	-	-	-	-	-	-
Rumex acetosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2m	-	-	-	-	-	-	-
Peucedanum cervaria	-	-	+	-	-	-	-	-	-	1	-	-	-	-	-	-	r	-	-	-	-	-
Bryophyta coll.	-	-	-	-	-	-	2m	2b	-	-	-	2a	3	-	-	-	-	-	-	-	-	-
Cytisus scoparius	-	-	-	-	-	r	3	1	-	+	4	+	4	-	r	R	-	2m	2a	r	-	-
Asparagus officinalis	r	-	-	-	-	-	-	-	-	-	r	-	-	r	r	-	-	r	-	-	-	-
Teucrium montanum	1	-	1	-	-	-	-	-	-	-	r	2m	2m	2a	1	-	r	-	-	-	1	-
Hypericum veronense	r	r	-	-	-	-	-	-	-	2m	-	r	r	1	-	-	r	-	-	-	-	-
Rumex thyrsiflorus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	r	-	-	-	-	-	-	-
Poa pratensis	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
Linaria genistifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	r	-	-	-	-	-	-	-	-
Galium verum	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
Festuca valesiaca	-	-	-	-	-	-	-	-	-	-	-	-	-	2b	1	-	-	-	-	-	-	-
Eryngium campestre	-	-	-	-	-	-	-	-	-	-	-	2a	-	r	-	-	-	-	-	-	-	-
Anthoxanthum odoratum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Verbascum lychnitis	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Potentilla arenaria	-	-	-	-	-	-	-	-	-	2m	-	-	-	-	-	-	-	-	-	-	-	-
Carex curvata	-	-	-	-	-	-	-	-	-	-	2m	-	-	-	-	-	-	-	-	-	-	-
Arrhenatherum elatius	-	-	-	-	-	-	r	-	-	-	1	-	-	2m	1	-	-	r	-	-	-	2m
Calamagrostis epigejos	-	-	-	-	-	-	-	r	+	1	1	5	3	5	-	5	5	2a	-	-	5	2a
Solidago gigantea	-	-	-	-	-	-	-	-	-	-	-	-	3	-	1	-	-	-	2a	4	2m	2b
Phytolacca americana	-	-	-	-	-	-	-	-	-	r	-	-	-	-	-	-	-	-	+	-	-	-
Sambucus nigra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	r	3	4	r	2a
Rubus fruticosus	-	-	-	-	-	-	-	-	-	r	r	-	-	-	-	-	2a	5	5	3	-	-
Galeopsis pubescens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	r	-	-
Chelidonium majus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	r	-	-
Urtica dioica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2m	2b
Robinia pseudaccacia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
Galium mollugo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2m
Galium aparine	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2m
Achilea millefolium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1

Appendix 2. Environmental table

	pH	Org. mat. mg/100g	Nitrogen mg/100g	TEB mval	HyA mval
site1	4.31	4140	0.60	18.24	51.38
site2	4.32	3800	0.00	17.66	56.25
site3	4.67	4890	0.53	20.54	39.75
site4	5.05	1650	0.00	17.86	15.38
site5	4.80	3680	0.00	23.81	42.00
site6	5.64	1310	0.00	17.86	9.38
site7a	5.43	1840	0.08	18.05	13.50
site7b	5.12	2080	0.09	18.24	21.38
site7c	5.02	2590	0.67	17.47	24.00
site8	4.55	3560	0.48	18.05	41.25
site9	5.07	2040	0.27	17.86	18.75
site10	4.56	2350	0.11	18.82	38.25
site11	4.73	3340	0.85	17.47	30.75
site12	4.46	3620	0.69	18.34	36.00
site13	5.16	1800	0.00	18.62	18.75
site14	5.19	1180	0.00	17.18	15.00
site15	4.96	4490	0.11	20.54	47.25
site16	4.97	2770	0.88	19.78	26.25
site17	4.88	1710	0.00	18.43	18.00
site18	4.27	4210	0.80	20.16	52.50
site19	4.77	3120	0.16	19.01	33.75
site20	4.56	5670	2.74	20.16	78.75