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Quantitative Analysis of the Xerothermic Grassland on the Boubová Hill (Bohemian Karst)

Kvantitativní analýza xerothermního porostu na Boubové v Českém krasu

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Abstract — Janko J. (1971): Quantitative analysis of the xerothermic grassland on the Boubová Hill (Bohemian Karst). — Preslia, Praha, 43 : 218—233. — Quantitative analysis of the xerothermic grassland on the southern slope of the Boubová Hill, Bohemian Karst, reveals an intricate pattern of single dominant populations, and mixed patches of positively associated species. The evaluation of quantitative characters shows that the majority of populations possess a contagious feature. In spite of the structural diversity, the entire grassland can be considered as a biologically integrated whole.

1 Introduction

The concepts and methods of the Zürich-Montpellier school predominating in Central European ecology and phytosociology provided a number of data on various vegetation types. The creation of a hierarchic classification system proved to be a most important step both in practical application and the development of further research. However, we cannot omit certain deficiencies in the concepts and methods of this school; a detailed structural analysis and sound of the vegetation — environment relationships requires a quantitative analysis using mathematico-statistical procedures (Kershaw 1964 : 134 sq.).

The present paper attempts to analyse the grassland on the Boubová Hill in the Bohemian Karst, Czechoslovakia. Similar vegetation was subject to numerous ecological studies (e.g. Klika 1928a, 1928b, 1942, etc.), and it remains in the focus of the interest of many botanists, as it represents a suitable basis for a discussion of fundamental ecological problems. The paper aims at the examination and application of quantitative methods in the research of xerothermic plant communities. The assessment of dominant populations, the characters of their structure, and mutual associations between populations of various species were the centre of general attention of the study.

2 Stand and sampling

The investigated grassland is situated on the southern slope of the Boubová Hill (alt. 427 m), Bohemian Karst, 30 km SW. of Prague. In the geographical respect, this locality belongs to the Karlštejn Plateau being a part of Beroun Highlands (Kodym et al. 1963), in the geological one, it belongs to the Silur-

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ian-Devonian basin of the Barrandien. Here the outcrops of the limestones of upper Silurian and lower Devonian appear forming shallow rendzina soils and bare rocks. The climate is moderately warm and moderately dry, with mildly cold winter. The annual mean temperature at the meteorological station of Králův Dvůr amounts to 8.4 °C, the mean annual total of precipitation is 481 mm (averages of fifty year period).

The subject of study was an isolated island of grassland vegetation, about 150 m long and 60 m wide, with the longer axis parallel to the contour lines, surrounded by xerothermic oak forest. The inclination of the slope aries from 10° to 30°. However, there are no sharp limits between the forest and grassland; a fairly complicated vegetational mosaic is encountered, here, so that classification of the stands according to formation types (e.g. DANSEREAU et ARROS 1959), on the basis of the structure (irrespective of its floristic composition and geographical position) meets with considerable difficulties. Particular patches of the area can be well called steppe, other parts meadow, parc or forest.

In the system of the Zürich-Montpellier school (KLIKA 1955) this grassland belongs to the class *Festuco-Brometea*, alliance *Festucion valesiacae*. However, in addition to elements of the above mentioned alliance, there are also elements of the class *Querco-Fagetea* (alliance *Quercion pubescentis*), class *Molinio-Arrhenathereteа* (alliance *Arrhenatherion elatioris*) and class *Trifolio-Geranietea sanguinei* (see MÜLLER 1962).

Under these circumstances an attempt to select "homogeneous and typical" sample plots and the assessment of the reasonable "minimal area" must inevitably fail (compare the account of the inaccuracy of this concept in HOPKINS 1957a). For this reason 3 larger sample plots, 30 by 30 m each, have been chosen after preliminary inspection of the entire area. Plot I included stand with "parc" characters (steppe with numerous isolated clumps of trees and shrubs), plot II covered mostly stand with steppe characters, and, finally plot III included a transition zone between steppe and forest.

The ecological differences between the above quoted 3 sample plots are well reflected in the soil conditions. In the plots I and II the soil type can be characterized as brown rendzina (PELÍŠEK 1961); in the plot III the soil type represents a transition to the brown-earth type. The soils of the non-forest stands are very shallow and contain a great proportion of skeleton; the upper layer is dark, humus-rich, mixed with remnants of plants, earth-worm castings, and game excrements. The soils within the forest part are deeper, and lighter in coloration, less stony, and poorer in organic increment.

In Tab. 1 some analytical data concerning the texture, specific gravity and pH of the soils in 3 sample plots are given. The texture of the fine-earth, prepared according to the international B-method, has been determined by sedimentation in Atterberg's cylinders (KLIKA, NOVÁK et GREGOR 1954 : 409). In each of the sample plots soil samples were taken at random from the depth

Tab. 1. — Physical characteristics of soils within the sample plots on the Boubová Hill

	Plot I	Plot II	Plot III
Texture			
Fraction I (to 0.01 mm)	24.84%	42.52%	33.68%
Fraction II (from 0.01 to 0.05 mm)	14.20	20.15	23.32
Fraction III (from 0.05 to 0.1 mm)	11.56	11.20	10.60
Fraction IV (from 0.1 to 2.0 mm)	49.40	36.13	34.20
Specific weight	1.84	2.01	2.50
Soil reaction (pH)	7.6	7.5	7.1

Tab. 2. — Life-form spectra for 3 sample plots on the Boubová Hill

	Plot I	Plot II	Plot III
Phanerophytes	11.9	5.2	17.6
Geophytes	6.1	7.0	10.8
Chamaephytes	15.3	19.2	17.6
Hemicryptophytes	51.4	45.8	44.5
Therophytes	15.3	22.8	9.5

of 15 cm. The specific gravity refers to the fine-earth of these samples. The soil reaction given in Tab. 1 represents an average of 5 random samples from each of the sample plots.

Measurements of the soil and air temperature, as well as measurements of evaporative power of air were carried out in summer 1964, showed considerable spatial variability within particular sample plots, so that in this respect a general differentiation between the 3 sample plots could not be established.

For the purpose of further ecological consideration the life-form spectra (prepared according to OBERDORFER 1962) give suitable background (Tab. 2). The differences are evident in the class of therophytes and phanerophytes. These differences can be statistically evaluated by a chi^2-test of independence

Tab. 3. — Numbers of species appropriate to different life-forms and sample plots (test of independence)

Life-forms		Plot I	Plot II	Plot III	Totals
Phanerophytes	observed	7	3	13	23
	expected	7.14	6.90	8.96	
	$(O-E)^2/E$	0.00	2.20	1.82	4.02
Geophytes	observed	4	4	9	17
	expected	5.28	5.10	6.62	
	$(O-E)^2/E$	0.31	0.24	0.86	1.41
Chamaephytes	observed	9	11	13	33
	expected	10.25	9.90	12.85	
	$(O-E)^2/E$	0.15	0.12	0.00	0.27
Hemicryptophytes	observed	30	26	32	88
	expected	27.33	26.40	34.27	
	$(O-E)^2/E$	0.26	0.01	0.15	0.42
Therophytes	observed	9	13	7	29
	expected	9.01	8.70	11.29	
	$(O-E)^2/E$	0.00	2.13	1.63	3.76
Totals	observed	59	57	74	190
	$(O-E)^2/E$	0.72	4.70	4.46	9.88

Note: O = observed value, E = expected value

(JANKO 1958 : 26). The corresponding contingency table is presented as Tab. 3. We can assume that owing to the mosaic character of the stand, and considerable mutual interaction of its populations, the grassland within the sample plots will biologically act as a whole, and the differences between its separate parts will not be substantial in this respect. The result of the test of indenpendence confirms this assumption: the summary of chi^2 at 8 degrees of freedom amounts to 9.88, which corresponds to 20%-level of statistical significance, and consequently, does not lead to a rejection of the presumptive null hypothesis. Similar conclusions can be drawn from the analysis of the ratio between genera and species: the generic coefficient (the number of genera expressed in % of the number of species — JACCARD 1932, GREIG-SMITH 1957: 133) amounts for the sample plot I to 84%, for plot II to 85%, and for plot III to 79%.

3 Dominance of species

The general appearance of a certain stand is, no doubt, affected by its species composition, however, this feature may not be decisive. Very important, too, is the number of plants of various species (size of the populations), the morphology of individual specimens, their distribution over the given area, etc. These aspects can be measured by means of the quantitative characters of the population (JENÍK 1964 : 40).

The most important of them is cover which also corresponds with the physiognomy of the stands. In our sample plots cover was measured by reading of the lengths occupied on linear transects of 1280 cm length; a total of 8 transects were placed in the sample plot II, in the sample plots I and III only 4 transects in each of them were studied. With their starting point determined at random, all transects were directed downward slope. Woody plants and cryptogams were excluded from the sampling. The results are shown in Tab. 4. Since the cover was measured in June and July, the data concenrning the cover values of therophytes are necessarily underestimated.

The quantitative character that can be most easily ascertained is the frequency. However, the results are affected by the size and number of the sampling quadrats. For this purpose small circular quadrats measuring 250 cm^2 were chosen. In each sample plot 100 of these sampling quadrats were placed at random; their centres were marked for the purpose of repeated sampling in various seasons of the year. In a similar way the density of populations was sampled, however, the respective sampling quadrats measured 50 cm^2 only. The number of "plant units", i.e. stalks, shoots, leaf-rosettes, leaves growing out of a rhizome, etc., were recorded in each sampling quadrat. In Tab. 5—7 the frequencies are given in the column F, the densities of single species for separate plots are presented in the column D.

From a comparison and evaluation of the quantitative characters mentioned above, the dominance of certain populations is also apparent. The term "dominance" has been used in various senses (GREIG-SMITH 1961a). In this paper, it is taken as a synthetic-character expressing the significant position of some populations in the investigated community. Dominant is a species that, within the given community, predominates by abundance, cover, and density. In the case of the xerothermic grassland on the Boubová hill, it is *Festuca valesiaca*, *Carex humilis*, *Teucrium chamaedrys*, *Potentilla aneraria*, *Thymus pulegioides* and *Poa pratensis* that occupy in all the sample plots a position of dominant species, which can often be recognized at first sight. In the sample plot III, additionally, *Fragaria viridis*, *Lathyrus niger*, *Hepatica nobilis*, *Viola hirta*, and, in the sample plots I and II ephemeral therophytes (namely *Thlaspi perfoliatum*) are met with as dominant plants.

Tab. 4. — Percentage cover for particular species of xerothermic grassland on the Boubová Hill

Species	Plot I	Plot II	Plot III
Achillea millefolium L.	1.68	0.67	2.02
Ajuga genevensis L.	0.01	—	0.00
Alyssum montanum L.	0.20	0.14	0.02
Anacamptis pyramidalis (L.) Rich.	0.00	—	—
Anemone nemorosa L.	—	—	0.06
Anthericum ramosum L.	0.00	—	0.07
Anthoxanthum odoratum L.	0.04	0.01	—
Arabis hirsuta (L.) Scop.	0.00	—	0.08
Arenaria serpyllifolia L.	0.21	0.26	0.00
Arrhenatherum elatius (L.) Presl	2.01	1.65	1.60
Artemisia campestris L.	0.35	2.49	—
Asperula cynanchica L.	0.21	0.11	0.46
Asperula glauca (L.) Bess.	6.58	2.46	0.50
Asperula tinctoria L.	0.03	—	0.18
Avenastrum pubescens (Huds.) Opiz	0.01	—	0.02
Brachypodium pinnatum (L.) P. Beauv.	0.03	—	0.23
Bupleurum falcatum L.	0.21	—	3.03
Calamintha clinopodium Spenner.	0.20	—	2.12
Carex humilis Leyss.	8.12	12.18	5.62
Carex muricata L.	0.01	—	0.02
Carex praecox Schreb.	0.13	—	—
Centaurea scabiosa L.	0.00	0.00	0.00
Centaurea stoebe (L.) Sch. Tell.	0.01	0.00	—
Centaurea triumfettii All.	0.00	—	—
Cerastium arvense L.	1.19	1.69	0.48
Chrysanthemum corymbosum L.	0.00	—	0.16
Coronilla varia L.	0.68	0.29	0.10
Dactylis glomerata L.	0.05	0.29	0.10
Dianthus carthusianorum L.	0.05	—	0.09
Dictamnus albus L.	0.01	—	0.09
Eryngium campestre L.	0.06	0.29	—
Euphorbia cyparissias L.	0.02	0.01	0.02
Fagopyrum convolvulus (L.) H. Gross	—	0.00	—
Festuca valesiaca Schleich.	26.00	28.23	11.06
Fragaria viridis Duch.	4.62	0.07	8.68
Galium aparine L.	0.15	0.07	0.25
Galium silvaticum L.	—	—	0.00
Geranium sanguineum L.	0.03	0.07	0.05
Helianthemum nummularium (L.) Mill.	0.48	0.43	0.23
Hepatica nobilis Mill.	0.80	—	2.86
Holosteum umbellatum L.	0.00	—	—
Hypericum perforatum L.	0.01	0.00	—
Inula hirta L.	—	—	0.05
Koeleria gracilis Pers.	0.63	0.09	—
Lathyrus niger (L.) Bernh.	—	—	2.81
Lathyrus pannonicus (Kram.) Garcke	0.14	—	1.14
Lathyrus vernus (L.) Bernh.	0.00	—	3.78
Linosyris vulgaris Cass.	2.46	1.74	0.34
Lithospermum arvense L.	1.01	1.15	0.01
Medicago falcata L.	0.07	0.06	0.08
Medicago minima (L.) Grufbg.	0.08	0.18	—
Melampyrum cristatum L.	—	—	0.23
Melica ciliata L.	0.03	0.24	—
Melica nutans L.	0.00	—	0.03
Origanum vulgare L.	0.00	0.06	—

Tab. 4 continued

Species	Plot I	Plot II	Plot III
Phleum boehmeri WIBEL.	2.13	1.08	0.08
Poa pratensis L.	8.01	5.15	1.01
Polygonatum odoratum (MILL.) DRUSE	2.13	1.73	0.51
Potentilla alba L.	0.00	—	0.00
Potentilla arenaria BORKH.	6.59	5.84	0.49
Primula veris L. em. HUDS.	—	—	3.03
Pulmonaria officinalis L.	—	—	0.40
Pulsatilla pratensis (L.) MILL.	0.23	0.01	0.04
Ranunculus bulbosus L.	—	0.00	—
Salvia pratensis L.	4.81	5.62	0.02
Scabiosa ochroleuca L.	0.65	0.81	0.00
Scabiosa columbaria L.	—	0.00	—
Sedum acre L.	1.02	0.82	0.02
Sedum album L.	0.00	0.02	—
Sedum sexangulare L.	4.75	4.69	0.37
Sedum telephium L.	0.00	—	0.00
Seseli osseum CR.	0.06	0.04	0.01
Sesleria calcarea (PERS.) OPIZ	0.00	—	—
Silene nemoralis W. K.	—	—	0.36
Stachys recta L.	1.43	1.47	0.20
Stellaria holostea L.	—	—	1.02
Stipa capillata L.	0.00	0.02	—
Taraxacum laevigatum (WILLD.) DC.	0.01	0.01	—
Teucrium chamaedrys L.	7.00	5.47	1.24
Thlaspi montanum L.	0.07	—	—
Thlaspi perfoliatum L.	0.09	0.03	—
Thymus pulegioides L.	9.17	8.73	0.99
Trifolium alpestre L.	0.19	0.00	1.07
Valerianella olitoria (L.) POLL.	0.12	0.16	0.00
Verbascum lychnitis L.	0.24	0.47	—
Veronica austriaca L.	—	—	0.00
Veronica hederifolia L.	0.26	0.68	0.09
Veronica spicata L.	0.00	—	—
Veronica teucrium L.	0.00	—	0.07
Vicia cracca L.	0.86	1.26	0.08
Vicia hirsuta (L.) S. F. GR.	0.18	0.80	—
Viola hirta L.	0.08	—	2.36
Without plant growth	18.51	24.21	41.73

On the basis of Raunkiaer's law of frequency (GREIG-SMITH 1957 : 16), the analysis of the frequency data mentioned above make it possible to check the right size of the sampling quadrats. GLEASON (1929) found out that the validity of this law is closely associated with the size of the sampling quadrats; if the sampling quadrats are too small, the number of species in the highest frequency class will decrease, or, there may be no species in that class at all, and vice versa. The Tab. 8 shows distribution of species within the sample plots into separate frequency classes, which proves that the size of the sampling quadrats (250 cm^2) used in the detection of frequency, was too small. In this way, more pronounced differentiation of populations with a greater frequency was made possible, on the other hand, the hierarchy in the less abundant species remained obscure (CAIN 1934). The effect of this methodical approach in establishing interspecific associations is reported in Chapter 5.

Tab. 5. — Values of frequency F, density D, its variance V, and coefficient of dispersion k in sample plot I

Species	F	D	V	k
Achillea millefolium L.	9	0.07	0.25	3.57
Alyssum montanum L.	11	0.23	1.31	5.70
Anacamptis pyramidalis (L.) RICH.	1	—	—	—
Anthoxanthum odoratum L.	4	—	—	—
Arenaria serpyllifolia L.	14	0.16	0.38	2.38
Arrhenatherum elatius (L.) PRESL	19	0.33	1.92	5.82
Asperula cynanchica L.	9	0.08	0.18	2.25
Asperula glauca (L.) BESS.	19	0.13	0.28	2.15
Asperula tinctoria L.	3	0.01	0.01	0.99
Aster amellus L.	2	—	—	—
Avenastrum pubescens (HUDS.) OPIZ	5	0.01	0.01	0.99
Carex humilis LEYSS.	55	1.51	14.46	9.57
Carex praecox SCHREB.	3	0.03	0.05	1.63
Centaurea stoebe (L.) SCH. TELL.	2	0.01	0.01	0.99
Centaurea triumfettii ALL.	1	—	—	—
Cerastium arvense L.	9	0.10	0.33	3.30
Coronilla varia L.	9	0.08	0.15	1.87
Dactylis glomerata L.	4	0.03	0.05	1.63
Eryngium campestre L.	4	—	—	—
Euphorbia cyparissias L.	16	0.18	0.80	4.44
Fagopyrum convolvulus (L.) H. GROSS	3	—	—	—
Festuca valesiaca SCHLEICH.	54	2.60	30.57	11.76
Fragaria viridis DUCH.	12	0.14	0.28	2.00
Helianthemum nummularium (L.) MILL.	9	0.10	0.19	1.90
Hepatica nobilis MILL.	8	0.04	0.04	0.98
Holosteum umbellatum L.	23	0.19	0.24	1.26
Koeleria gracilis PERS.	11	0.23	0.24	1.26
Linosyris vulgaris CASS.	21	0.36	1.08	3.00
Lithospermum arvense L.	19	0.25	0.76	3.01
Melica nutans L.	6	0.04	0.04	0.98
Myosotis hispida SCHLECHT.	16	0.20	0.28	1.40
Myosotis silvatica (EHRH.) HOFM.	7	0.06	0.14	2.33
Phleum boehmeri WIBEL.	10	0.05	0.25	5.00
Poa pratensis L.	28	0.89	7.62	8.56
Polygonatum odoratum (MILL.) DRUCE	13	0.11	0.25	2.27
Potentilla arenaria BORKH.	38	1.01	4.86	4.81
Pulsatilla pratensis (L.) MILL.	6	0.01	0.01	0.99
Salvia pratensis L.	10	0.04	0.04	0.97
Sedum acre L.	15	0.46	2.49	5.41
Sedum sexangulare L.	31	0.75	5.89	7.85
Seseli osseum CR.	7	0.01	0.01	0.99
Sesleria calcarea (PERS.) OPIZ.	2	—	—	—
Stachys recta L.	20	0.31	0.90	2.20
Taraxacum laevigatum (WILLD.) DC.	1	—	—	—
Teucrium chamaedrys L.	65	1.27	5.97	4.70
Thlaspi montanum L.	10	0.07	0.25	3.57
Thlaspi perfoliatum L.	89	1.46	5.43	3.72
Thymus pulegioides L.	47	0.93	5.58	6.00
Trifolium alpestre L.	5	0.03	0.03	0.98
Valerianella olitoria (L.) POLL.	33	0.71	2.67	3.76
Veronica hederifolia L.	18	0.23	0.51	2.13
Veronica praecox ALL.	12	0.08	0.18	2.25
Vicia cracca L.	20	0.22	0.88	4.00
Vicia hirsuta (L.) S. F. GR.	12	0.06	0.10	1.61
Viola hirta L.	8	0.03	0.03	0.98

Tab. 6. — Values of frequency *F*, density *D*, its variance *V*, and coefficient of dispersion *k* in sample plot II

Species	F	D	V	k
Achillea millefolium L.	10	0.03	0.03	0.98
Alyssum montanum L.	11	0.12	0.35	2.92
Anthericum ramosum L.	1	—	—	—
Arabidopsis thaliana (L.) HEYN.	3	0.01	0.01	0.99
Arenaria serpyllifolia L.	7	0.04	0.10	2.48
Arrhenatherum elatius (L.) PRESL	21	0.13	0.60	4.62
Artemisia campestris L.	13	0.02	0.04	1.98
Asperula cynanchica L.	4	0.03	0.03	0.98
Asperula glauca (L.) BESS.	18	0.10	0.19	1.90
Carex humilis LEYSS.	81	1.75	8.42	4.81
Cerastium arvense L.	10	0.12	0.33	2.75
Coronilla varia L.	3	0.01	0.01	0.99
Dianthus carthusianorum L.	11	0.08	0.15	1.87
Erophila verna (L.) F. CHEV.	4	0.02	0.04	1.98
Eryngium campestre L.	6	0.01	0.01	0.99
Euphorbia cyparissias L.	7	0.04	0.10	2.48
Fagopyrum convolvulus (L.) H. GROSS	2	—	—	—
Festuca valesiaca SCHLEICH.	70	2.70	21.07	7.80
Fragaria viridis DUCH.	2	—	—	—
Geranium sanguineum L.	3	—	—	—
Helianthemum nummularium (L.) MILL.	10	0.10	0.19	1.86
Holosteum umbellatum L.	6	0.05	0.06	1.34
Hypericum perforatum L.	1	—	—	—
Koeleria gracilis PERS.	16	0.28	1.42	5.07
Linosyris vulgaris CASS.	14	0.07	0.13	1.86
Lithospermum arvense L.	36	0.51	1.65	3.23
Medicago falcata L.	2	—	—	—
Medicago minima (L.) GRUFBG.	9	0.06	0.08	1.27
Melica ciliata L.	6	0.09	0.28	3.11
Myosotis hispida SCHLECHT.	17	0.08	0.07	0.87
Myosotis silvatica (EHRH.) HOFM.	4	0.03	0.03	0.98
Phleum boehmeri WIBEL.	9	0.05	0.17	3.40
Poa pratensis L.	35	1.04	4.24	4.08
Polygonatum odoratum (MILL.) DRUCE	6	0.02	0.02	0.98
Potentilla arenaria BORKH.	38	0.92	3.81	4.14
Ranunculus bulbosus L.	4	—	—	—
Salvia pratensis L.	11	0.03	0.03	0.98
Scabiosa canescens W. K.	1	—	—	—
Scabiosa ochroleuca L.	10	0.06	0.10	1.61
Sedum acre L.	17	0.25	0.88	3.52
Sedum album L.	6	0.12	0.49	4.08
Sedum sexangulare L.	28	0.72	3.47	4.82
Stachys recta L.	20	0.16	0.26	1.63
Stipa capillata L.	4	0.04	0.10	2.48
Taraxacum laevigatum (WILLD.) DC.	5	0.01	0.01	0.99
Teucrium chamaedrys L.	43	0.78	2.68	3.44
Thlaspi perfoliatum L.	52	0.58	2.28	3.93
Thymus pulegioides L.	48	1.14	8.16	7.16
Valerianella olitoria (L.) POLL.	22	0.41	3.72	9.07
Verbascum lychnitis L.	1	—	—	—
Veronica hederifolia L.	20	0.24	0.52	2.17
Veronica praecox ALL.	20	0.10	0.12	1.20
Vicia cracca L.	18	0.23	0.72	3.13
Vicia hirsuta (L.) S. F. GR.	21	0.24	0.52	2.17

Tab. 7. — Values of frequency F, density D, its variance V, and coefficient of dispersion k in sample plot III

Species	F	D	V	k
Achillea millefolium L.	21	0.26	0.43	1.65
Ajuga genevensis L.	3	0.02	0.04	1.98
Alyssum montanum L.	5	0.02	0.02	0.98
Anemone nemorosa L.	6	0.02	0.02	0.98
Anthericum ramosum L.	7	0.02	0.02	0.98
Arabis hirsuta (L.) SCOP.	8	0.08	0.07	0.87
Arrhenatherum elatius (L.) PRESL	16	0.16	0.41	2.60
Asperula cynanchica L.	31	0.28	0.37	1.42
Asperula glauca (L.) BESS.	19	0.24	0.40	1.65
Asperula tinctoria L.	15	0.08	0.07	0.87
Aster amellus L.	5	0.04	0.10	2.48
Avenastrum pubescens (HUDS.) OPIZ	5	0.02	0.4	1.98
Brachypodium pinnatum (L.) P. BEAUV.	7	0.9	0.20	2.22
Bupleurum falcatum L.	21	0.16	0.14	0.84
Calamintha clinopodium SPENNER.	21	0.28	0.45	1.61
Carex humilis LEYSS.	34	1.16	7.68	6.62
Carex leporina L.	7	0.14	0.42	3.01
Carex muricata L.	1	—	—	—
Cerastium arvense L.	12	0.14	0.39	2.10
Chrysanthemum corymbosum L.	6	0.02	0.02	0.98
Coronilla varia L.	7	0.04	0.04	0.98
Dactylis glomerata L.	6	0.01	0.01	0.99
Dianthus carthusianorum L.	3	0.01	0.01	0.99
Dictamnus albus L.	3	—	—	—
Euphorbia cyparissias L.	2	—	—	—
Festuca valesiaca SCHLEICH.	61	2.20	17.97	8.17
Fragaria viridis DUCH.	48	0.68	1.09	1.60
Galium aparine L.	8	0.03	0.03	0.98
Galium silvaticum L.	2	—	—	—
Geranium sanguineum L.	5	0.01	0.01	0.99
Helianthemum nummularium (L.) MILL.	6	0.04	0.04	0.98
Hepatica nobilis MILL.	36	0.30	0.30	1.00
Holosteum umbellatum L.	1	—	—	—
Inula hirta L.	5	0.02	0.04	1.98
Inula salicina L.	1	—	—	—
Lathyrus niger (L.) BERNH.	28	0.30	0.44	1.48
Lathyrus pannonicus (KRAM.) GARCKE	10	0.11	0.25	2.27
Lathyrus vernus (L.) BERNH.	13	0.12	0.19	1.62
Melampyrum cristatum L.	8	0.06	0.08	1.27
Melica nutans L.	8	0.04	0.10	2.48
Poa pratensis L.	11	0.10	0.19	1.86
Polygonatum odoratum (MILL.) DRUCE	9	0.02	0.02	0.98
Potentilla alba L.	2	—	—	—
Potentilla arenaria BORKH.	13	0.31	1.40	4.52
Primula veris L. em. HUDS.	14	0.10	0.09	0.90
Pulsatila pratensis (L.) MILL.	4	0.02	0.02	0.98
Sedum sexangulare L.	15	0.31	1.61	5.20
Silene nemoralis W. K.	8	0.04	0.04	0.97
Stellaria holostea L.	16	0.18	0.22	1.22
Teucrium chamaedrys L.	7	0.07	0.13	1.86
Thlaspi perfoliatum L.	25	0.43	1.81	4.21
Thymus pulegioides L.	22	0.57	3.59	6.13
Trifolium alpestre L.	23	0.22	0.23	1.05
Valerianella olitoria (L.) POLL.	6	0.04	0.10	2.48
Veronica austriaca L.	1	—	—	—

Tab. 7 continued

Species	F	D	V	k
Veronica hederifolia L.	18	0.19	0.34	1.80
Veronica praecox ALL.	8	0.04	0.04	0.97
Veronica spicata L.	2	—	—	—
Veronica teucrium L.	7	0.04	0.10	2.48
Vicia cracca L.	6	—	—	—
Viola hirta L.	30	0.29	0.32	1.10

4 Pattern

Pattern, or also dispersion (JENÍK 1964) may be defined as a departure from randomness in the distribution of members of investigated populations. It belongs to the most valuable characters from the ecological point of view, indicating both morphological features and the activity of the controlling environmental factors*. On the assumption of random distribution of indi-

Tab. 8. — Distribution of species into frequency classes in %

Frequency class	Plot I	Plot II	Plot III
I. from 0 to 20%	76.3	72.3	78.8
II. from 21 to 40%	14.6	18.5	18.0
III. from 41 to 60%	5.5	5.6	1.6
IV. from 61 to 80%	1.8	1.8	1.6
V. from 81 to 100%	1.8	1.8	—

vidual plants in the investigated area, we can expect the same random distribution in the sampling quadrats, placed themselves at random. A departure from randomness can be tested in different ways, but it is the test of the goodness of fit (GREIG-SMITH 1957: 57 et 62) that is considered as the most reliable method. This test consists in comparison of observed values with values expected on the basis of Poisson's distribution. For this purpose density data were used, and the test of goodness of fit was calculated for 17 populations. The values of chi^2 in all the cases made it possible to reject the hypothesis concerning the goodness of fit of observed numbers of quadrats with 0, 1, 2 . . . "plant units" with theoretical numbers, at a high level of statistical significance. This was applied to populations of *Festuca valesiaca*, *Carex humilis*, *Linosyris vulgaris*, *Poa pratensis*, *Potentilla arenaria*, *Sedum acre*, *Sedum sexangulare*, *Teucrium chamaedrys*, *Thymus pulegioides*, *Thlaspi perfoliatum*, *Valerianella olitoria* and *Fragaria viridis* (some of them repeatedly in more sample plots).

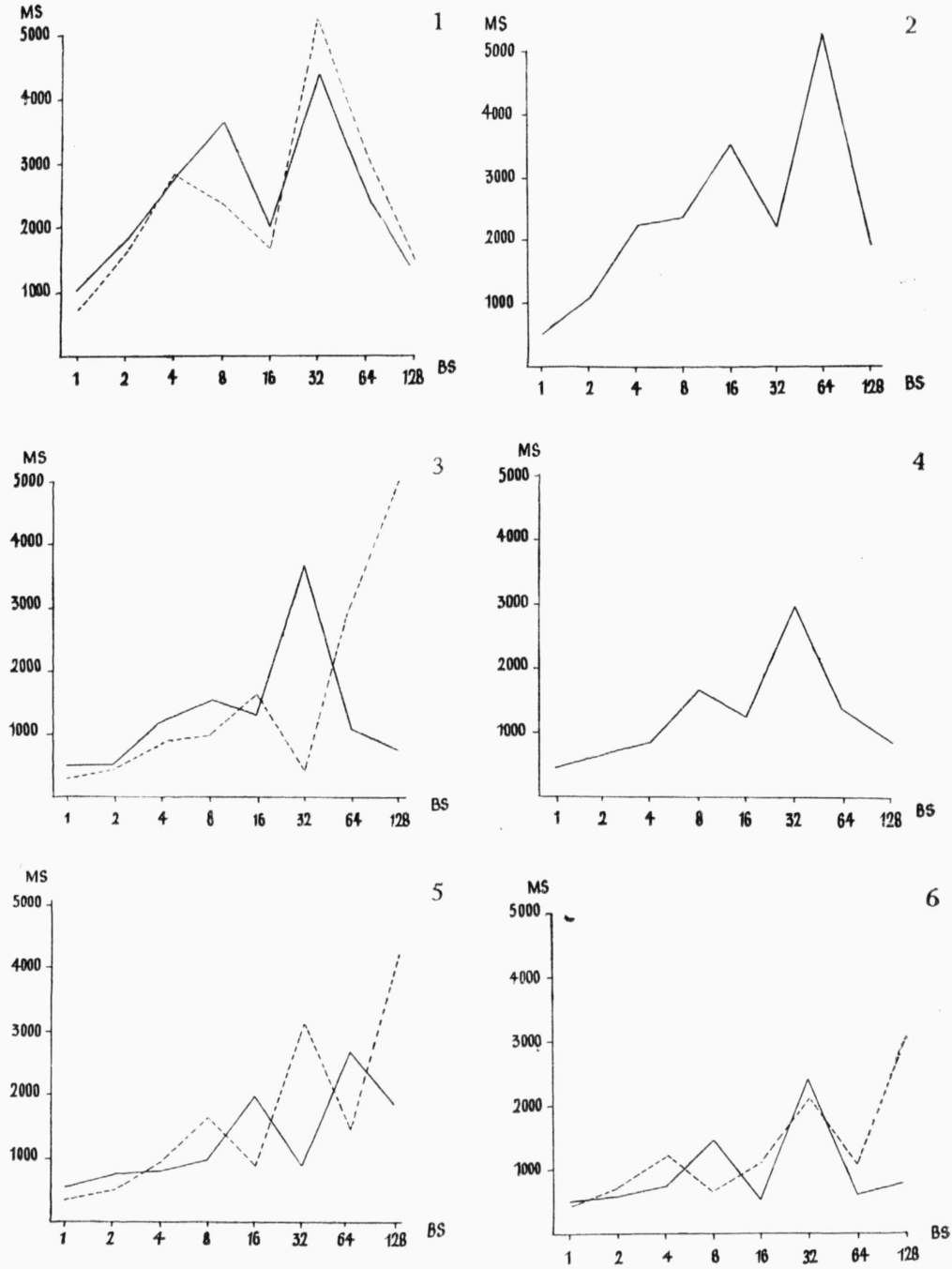
Departures from the random distribution can be further differentiated: a population with one type of departure are marked as contagious (also

* It was SCHUSTLER (1922) who, explaining the concept "repartice", actually anticipated the meaning of the concept "pattern".

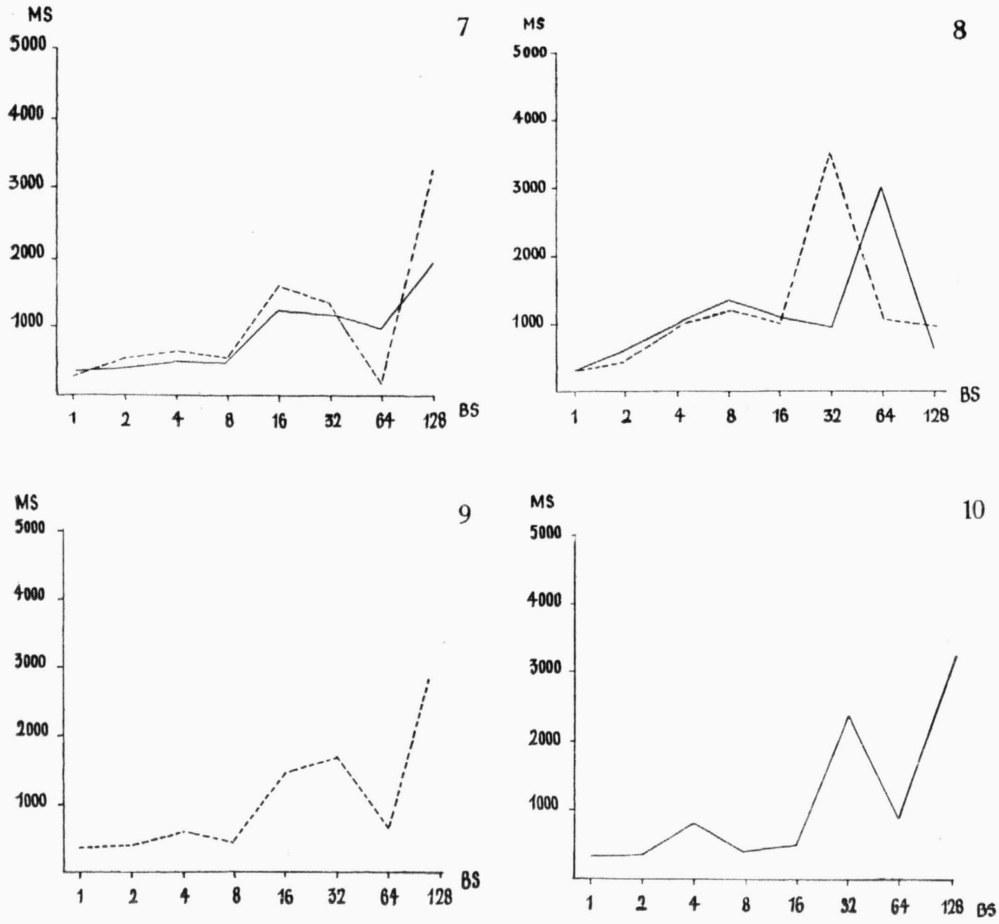
overdispersed, aggregated), a population with another type of departure as regular (underdispersed). An appropriate criterion that makes it possible to differentiate 3 types of populations — random, contagious and regular — used here is the ratio of the variance of density to its mean. BLACKMAN (1942) gave the name of coefficient of dispersion to this quantity; this coefficient is to be found in Tab. 5, 6 and 7, in column marked "k"; at the same time, the variance of density "V" is given in the same table. The coefficient of dispersion gets the value 1 for random populations, for contagious populations it is higher than 1; and for regular populations it is lower than value 1. This coefficient can be statistically tested by means of the t-test (GREIG-SMITH 1957 : 181). By a described procedure, confidence bands at the 5% level of statistical significance were obtained; for all the values "k" included within the confidence bands, we accept the hypothesis that they do not differ significantly from 1, the values outside the bands indicate contagious or regular populations. The calculated limits amount to 0.713 and 1.281. The evaluation of coefficients of dispersion brought the following results: in populations of the sample plot I, the ratio of random populations to contagious ones was 10 : 37, in the sample plot II, it was 12 : 33; and in the sample plot III the ratio was 22 : 29. At the 5%-level of statistical significance, not a single population could be characterized as a regular one. The predominance of non-randomness, proved for some selected populations by the test of goodness of fit, has been confirmed in the highest degree by the coefficients of dispersion namely for dominant populations. Also, it seems that the influence of the forest (in the sample plot III) moderates the extreme activity of certain controlling environmental factors, and supports the random distribution of members of various populations.

Of fundamental significance for the detection of pattern is the important method that has been originally formulated by GREIG-SMITH (1952) for the analysis of the population density data, and that has been adapted by KERSHAW (1957) for processing data concerning frequency and cover. This method very much faciliated the procedure. The main contribution of this method (called "dimensional analysis" by KERSHAW) is the possibility of ascertaining the size of the source of the vegetational heterogeneity (in our case, the size of the patches of individuals forming a certain population). The data concerning the cover (cover data in basic units, see below) are joined into blocks gradually containing as many as 2^n of basic units, and the variance of data about cover is analysed. The results may be plotted on the graph of mean square against block size; the block size showing peak corresponds to the average linear dimension of the source of heterogeneity in the field.

For the dimensional analysis, transects in the sample plots I and II were used (see Chapter 3), in addition, in the sample plot II 4 new transects were placed at right angles to the position of the 8 original transects, i.e. parallel to the contour lines. The size of the basic unit was 5 cm; at each whole cm (as a subunit) the occurrence of species was recorded in terms presence—absence. Each of the transects contained a total of 256 basic units (the length amounted to 1280 cm). The selection of species for dimensional analysis was limited by the 5%-minimum of cover (KERSHAW 1957); in "contour lines transects" in the plot II, data were established only for *Festuca valesiaca*



Figs. 1–6. — Graphs of mean square (MS) against block size (BS) for dimensional analysis of pattern. The broken line: sample plot I, the solid line: sample plot II. — 1: *Festuca valesiaca*; 2: *F. valesiaca*, additional sampling; 3: *Carex humilis*; 4: *C. humilis*, additional sampling; 5: *Poa pratensis*; 6: *Potentilla arenaria*.



Figs. 7—10. — Graphs of mean square (MS) against block size (BS) for dimensional analysis of pattern. The broken line: sample plot I, the solid line: sample plot II. — 7: *Teucrium chamaedrys*; 8: *Thymus pulegioides*; 9: *Asperula glauca*; 10: *Salvia pratensis*.

and *Carex humilis* which were the most important populations in the stand. The results of the dimensional analysis are shown in Figs. 1—10 which have the form of graphs of mean square against block size, for *Festuca valesiaca*, *Carex humilis*, *Poa pratensis*, *Potentilla arenaria*, *Teucrium chamaedrys*, *Thymus pulegioides*, *Asperula glauca* and *Salvia pratensis*. A survey of the scale of heterogeneity of various populations in cm is given in Tab. 9.

Comparing the scales of heterogeneity in the same species from both sampled plots, we can see that some populations maintain the same heterogeneity scale (e.g. *Teucrium chamaedrys*, partly *Potentilla arenaria* and *Festuca valesiaca*), while others are different as to their heterogeneity (*Carex humilis*, *Poa pratensis*). A dimensional analysis carried out in two directions demonstrated a uniformity of size of heterogeneity sources in *Carex humilis*; in *Festuca valesiaca*, on the other hand, an increase in size of a smaller source of heterogeneity in the direction of contour lines appeared. An analysis of

Tab. 9. — Linear scales of pattern

Species	Sample plot	Block size in cm							
		5	10	20	40	80	160	320	640
Festuca valesiaca	I.			+			+		
Festuca valesiaca	II.				+		+		
Festuca valesiaca	II. A					+		+	
Carex humilis	I.					+			+
Carex humilis	II.				+		+		
Carex humilis	II. A				+		+		
Asperula glauca	I.			+			+		+
Poa pratensis	I.				+		+		+
Poa pratensis	II.					+		+	
Potentilla arenaria	I.			+			+		+
Potentilla arenaria	II.				+		+		
Salvia pratensis	II.			+			+		+
Teucrium chamaedrys	I.			+		+			+
Teucrium chamaedrys	II.			+		+			+

Note: "A" in the column "sample plot" indicates the additional sampling "contour line transects".

variance in tussocks of the latter species according to lines and column (Fabian 1963 : 173) suggests that a certain zonation along the contour lines takes place, here.

Unfortunately, similar dimensional analysis could not be carried out in the habitat factors (Boubová Hill is in a natural reservation), which could reveal the possible causes of heterogeneity sources of the said populations in the grassland. Thus, one can only state that in populations showing patches of individuals of a rather smaller size (e.g. *Festuca valesiaca*) the heterogeneity in most cases is influenced by morphological features (the size of tussocks, the way of vegetative reproduction, etc.), while in populations with more spacious patches the heterogeneity is influenced, above all, by different activity of environmental factors.

5 Associations between species

Mutual relations of various populations in the grassland, quantitatively expressed in form of objectively defined interspecific associations, are an important character of the community which makes any classification of the vegetation more reasonable. To find them out, the chi^2-test of independence (Greig-Smith 1957 : 87) of joint occurrences from frequency data has been used. Only mutual relations of species with a minimal frequency of 10% were evaluated. This condition is fulfilled by 29 species in the sample plot I and II, and by 25 species in the sample plot III.

On the whole, 12 groups of positively associated species at the 5%-level

of statistical significance have been found, of which 5 in the sample plot I, 4 in plot II, and 3 in plot III. Only 6 groups of positively associated species reached the extent of at least 5 species. These are:

In the sample plot I:

1. *Alyssum montanum, Euphorbia cyparissias, Lithospermum arvense, Potentilla arenaria, Sedum sexangulare, Thymus pulegioides*;
2. *Arenaria serpyllifolia, Poa pratensis, Sedum acre, Valerianella olitoria, Vicia cracca.*

In the sample plot II:

3. *Achillea millefolium, Alyssum montanum, Arrhenatherum elatius, Cerastium arvense, Lithospermum arvense, Veronica hederifolia*;
4. *Carex humilis. Festuca valesiaca, Potentilla arenaria, Sedum sexangulare, Teucrium chamaedrys, Thlaspi perfoliatum, Thymus pulegioides*;
5. *Asperula glauca, Linosyris vulgaris, Poa pratensis, Sedum acre, Stachys recta, Vicia cracca, Vicia hirsuta.*

In the sample plot III:

6. *Asperula tinctoria, Calamintha clinopodium, Fragaria viridis, Hepatica nobilis, Trifolium alpestre, Viola hirta.*

All of these groups of species are weakly integrated; taking the measure of integrity of groups to the relationship between the number of associations and the number of species $A : S$ (symbolics according to HOPKINS 1957b), it is group 4 that is the integrated one. However, its degree of integrity reaching 1.29 only, is fairly low in comparison to HOPKINS' material.

The interpretation of the above quoted interspecific associations and the groups of positively associated species is very difficult. The small size of the sampling quadrats used in sampling of frequency influenced the ascertaining of the positive interspecific associations: the criteria for their recognition were stricter than in larger quadrats. Consequently, a greater number of small groups and lower degree of their integrity appeared in our results. This may mean, on the one hand, a true comprehension of the close mutual relationships of populations, on the other hand, a deformation of these relationships by recording of greater influences of local fluctuations in pattern, morphological features of individuals, etc. To solve these questions more satisfactorily, a comparison of the degree of interspecific associations determined by means of several sets of sampling with different size of quadrats (HOPKINS 1957b) would be necessary.

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Souhrn

Kvantitativní analýza xerothermního porostu na kopci Boubová v Českém krasu prokázala komplikovanou strukturu, vytvářenou jednak mozaikou shluků jedinců téže populace, jednak skupinami jedinců většího počtu pozitivně sdružených populací. Analýza pokryvnosti, frekvence a denzity umožnila stanovit dominantní populace. Při zkoumání charakteru disperze těchto dominantních populací byl jednoznačně prokázán kontagiózní charakter. Naproti tomu interpretace objektivně zjištěných skupin pozitivně sdružených populací nevede k jednoznačným závěrům a vyžaduje si dalšího šetření. Při vší floristické a strukturální rozmanitosti vyšetřovaného porostu analýza opravňuje k opatrným závěrům o jeho biologické celistvosti. — Vedle

vlastní kvantitativní analýzy porostu na Boubové bylo cílem práce ověřit možnost aplikace některých kvantitativních metod, vyvinutých především anglosaskými autory, na středoevropskou vegetaci.

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