Preslia, Praha, 58 : 55—62, 1986

Vegetational changes on permanent plots in a steppe community

Změny vegetace na trvalých plochách ve stepním společenstvu

Zdenka Hroudová and Karel Prach

HROUDOVÁ Z.[1]) et PRACH K.[2]) (1986): Vegetational changes on permanent plots in a steppe community. — Preslia, Praha, 58 : 55—62.

Changes of a steppe community in the Bohemian Karst, ČSSR, were assessed by means of vegetation analysis on permanent quadrats, using "micromaps". Cover values of main participant species (*Festuca valesiaca, F. rupicola, Carex humilis*) were compared year by year in the periods between 1965 to 1967, and 1979 to 1982, and related to climatic fluctuations. No directional (successional) changes were apparent, comparing the two periods of surveying. Results are commented from the point of view of autecology and population ecology of participant species, on the background of the Central European "steppe problem".

Institute of Botany, Czechoslovak Academy of Sciences, 252 43 Průhonice[1]), *and 379 82 Třeboň*[2]), *Czechoslovakia.*

The "steppe" question has been for a long time one of the interesting topics of Central European geobotanists, see JENÍK (1969), MORAVEC (1970), MARTINOVSKÝ et KOLBEK (1984), etc. There are studies utilising data of paleobotany, quaternary geology or indirect historical information in order to clarify the origin and development of small grassland islands within the closed-canopy forests, see LOŽEK (1971). Also, we have got studies describing the present state of steppe communities in detail (e.g., SLAVÍKOVÁ 1982). However, we especially lack studies in quantitative terms evaluating the vegetational changes in steppe communities during a period of several years or decades. Such information could give us a valuable insight into the current dynamics of these communities, and enable our better understanding of their past development.

METHODS AND STUDY SITE

In 1965, the former author marked four permanent plots 1 × 1 m on the Strážiště Hill in the Bohemian Karst, and made "micromaps" (PUČELÍKOVÁ 1967, HROUDOVÁ-PUČELÍKOVÁ 1972). In the spring 1979, we have successfully recovered all these plots, and have repeatedly drawn the "micromaps" in the following years, 1979 to 1982. This enabled us to compare the present distribution and cover degree of the main participating species, with their situation 17 years ago, as well as to evaluate year by year their changes and to relate them to the climatic conditions in the particular years.

The "micromaps" were drawn by means of a woody frame divided into a net of 20 to 20 cm by iron sticks, in August. The cover values were obtained from "micromaps" by a hand planimeter. Margines of particular specimens, deliminated by compact tussocks, were considered.

The Strážiště Hill (440 m a.s.l.) is located 2.5 km to the south of the Srbsko railway station about 30 km southwest of Prague. The steppe covers an area of about 1500 m^2, and it is placed on the southern and southwestern slopes inclined 16 to 20°, close to the summit of the limestone hill. Rendzina is the soil type here, with an average depth of 5.8 cm of the stoneless top soil,

Table 1. — Occurrence of plant species on four permanent quadrats in the period of 1965—67 (a) and of 1979—82 (b). The nomenclature is after NEUHÄSLOVÁ et KOLBEK (1982).

No. of quadrat:	1.		2.		3.		4.	
	a	b	a	b	a	b	a	b
Festuca valesiaca	+	+	+	+	+	+	+	+
Carex humilis	+	+	+	+	+	+	+	+
Teucryum chamaedrys	+	+	+	+	+	+	+	+
Coronilla varia	+	+	+	+	+	+	+	+
Hypericum perforatum	+	+	+	+	+	+	+	+
Koeleria macrantha	+	+	+	+	+	+	+	+
Helianthemum nummularium	+	+	+	+	+	+	+	+
Potentilla arenaria	+	+	+	+	+	+	+	+
Anthericum ramosum	+	+	+	+	+	+	+	+
Verbascum lychnitis	+	+	+	+	+	+		+
Pseudolysimachion spicatum			+	+	+		+	+
Myosotis stricta	+		+	+			+	
Echium vulgare			+	+		+	+	+
Festuca rupicola					+	+		
Sedum sexangulare	+	+						
Sanguisorba minor	+	+						
Thymus pulegioides							+	+
Asperula cynanchica					+	+		+
Thlaspi perfoliatum		+				+		
Taraxacum officinale agg.				+				+
Cuscuta epithymum				+				+
Viola arvensis				+				
Salvia pratensis						+		
Poa angustifolia						+		
Pulsatilla pratensis			+					
Centaurea rhenana							+	
Scabiosa ochroleuca							+	

and with fissures in the limestone rock reaching a depth of about 25 to 30 cm. The steppe "island' is surrounded by a oak-hornbeam forest, with a high occurrence of shrubs (*Cotoneaster integerrimus*, *Crataegus* sp., *Sorbus aria*, *S. torminalis*, *Cornus mas*), especially on the forest margine. *Quercus pubescens* is also present, several specimens are scattered in the steppe area, too.

The steppe vegetation on the Strážiště Hill can be classified in the scope of all. *Festucion valesiacae* KLIKA 1931, as a transitional type between ass. *Erysimo crepidifolii-Festucetum valesiacae* KLIKA 1933 and ass. *Carici humilis-Festucetum sulcatae* KLIKA 1951. The species composition of our permanent quadrats is apparent from Table 1.

ECOLOGICAL PROPERTIES OF THE DOMINANT SPECIES (IN CENTRAL BOHEMIA)

Festuca valesiaca is the main dominant species on our permanent quadrats. It is characterized by following properties:

- it has high requirements for light
- it occurs predominantly on basic soil, rarely on sites with acid parent material
- it prevails on dry and warm slopes exposed to strong insolation (JENÍK et REJMÁNEK 1969)
- it is able to survive short-term, extremly high temperatures
- it grows well even on deeper soil layer, where the water supply is sufficient, but on these sites it is suppressed by other stronger competitors, e.g., *Festuca rupicola*, *Poa angustifolia*, *Brachypodium pinnatum*).

The habitat of *Festuca valesiaca* on the Strážiště Hill exhibits a rather deeper soil layer, and extremely high temperatures during warm periods, especially at the soil surface — see HROUDOVÁ-PUČELÍKOVÁ (1972). It seems to be favourable for the development of *Festuca valesiaca:* its roots reach fissures among rocks to the depth of 25—30 cm, some of them deeper in crevices into the parent rock, where the soil moisture is sufficient. At the same time, a dry period supresses other competitively stronger species. In the Bohemian Karst, *Festuca valesiaca* represents a dominant species of the most xerothermic steep slopes exposed predominantly to the S (SE — SW). It does not occure on wind-exposed west slopes.

Carex humilis, the second dominant species, can be characterized as follows (according to SMETÁNKOVÁ 1959):

— it shows high requirements for light, but occurs also at the ground layer of forests of the suball. *Quercenion pubescentis* KLIKA 1957
— though considered as a calciphyte, in some cases it occurs on acid soils, too
— production of the biomass and seed production show that the most favourable conditions for its growth are steppe habitats with full insolation and with a continuous soil layer
— in these optimum habitats, *Carex humilis* does not usually reach a high degree of abundance, because it is suppressed by stronger competitors.

Carex humilis represents a constant participant of the steppe communities in the region, where the open cover of the community seems to be favourable for its growth.

Festuca rupicola can be characterized by the following properties (for further information see SLAVÍKOVÁ et al. 1984):

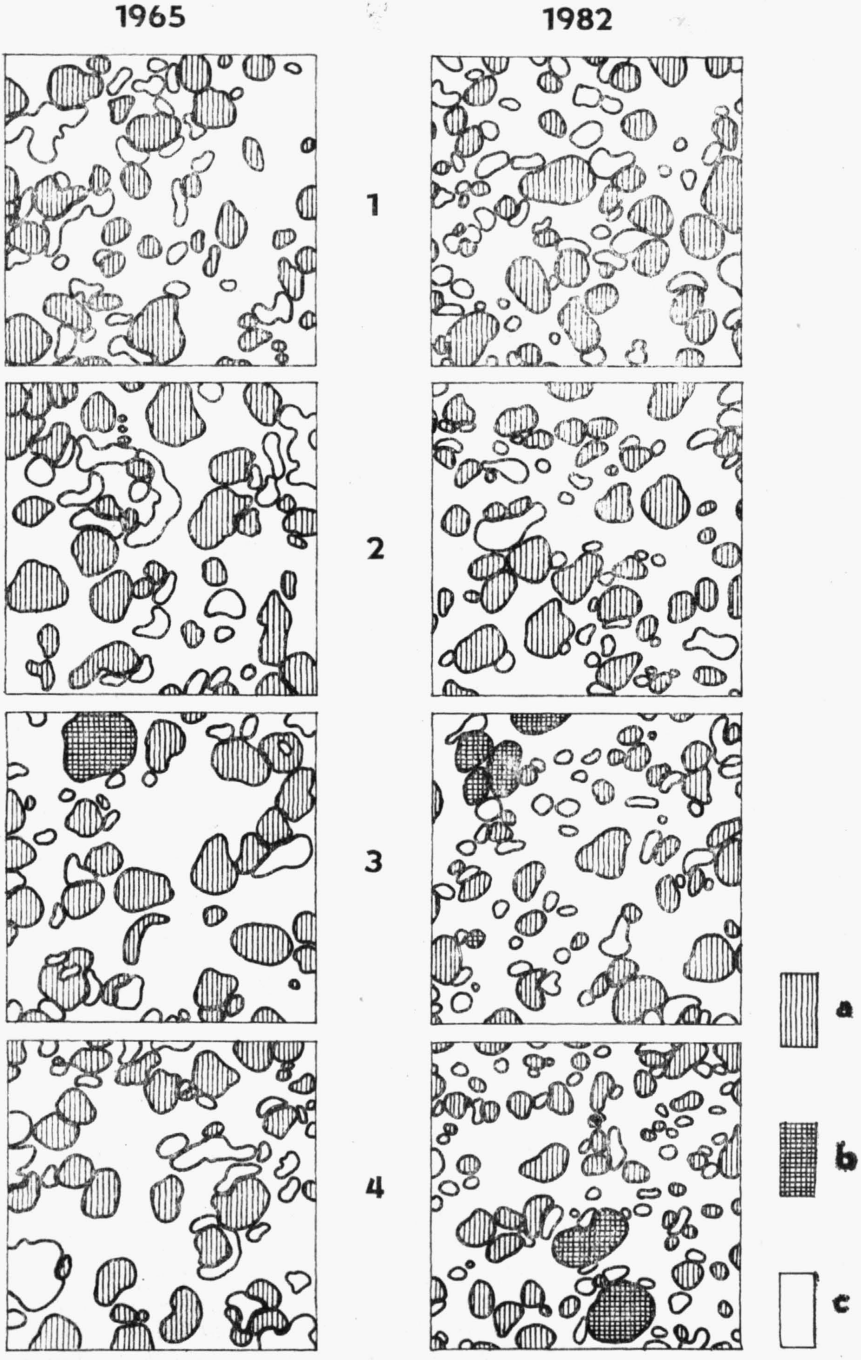
— it has high requirements for light, too
— its occurrence is not restricted on alkaline substrata; it can grow on neutral or acid soils; in this respect, *F. rupicola* shows wider ecological amplitude than *F. valesiaca*
— it grows on deeper soil of more mesophytic habitats than the other two species
— on such sites, *F. rupicola* is able better to utilize the water content in the soil, and seems to be a stronger competitor than *F. valesiaca*
— on the other hand, *F. rupicola* is irreversibly damaged by short-term, extremly high temperatures (see PUČELÍKOVÁ 1967, RAMBOUSKOVÁ 1981).

In the Bohemian Karst, *F. rupicola* often grows in steppe communities where it usually replaces *F. valesiaca* under more mesic conditions.

RESULTS AND DISCUSSION

Distribution of *Festuca valesiaca*, *F. rupicola*, and *Carex humilis* on all four permanent quadrats in 1965, in comparison with that in 1982, is demonstrated in Fig. 1. It is hardly possible to identify particular tussocks but the general distribution of them is simillar both in 1965 and 1982.

The sole original large tussock of *F. rupicola* (1965, plot no. 3) was found to be split in two parts in 1979, and in the following years desintegrated into several smaller parts. Two large tussocks of *F. rupicola* have newly arisen since 1967 in the no. 4 quadrat probably as a result of more humid and cold


1965
1982
1
2
3
4
a
b
c

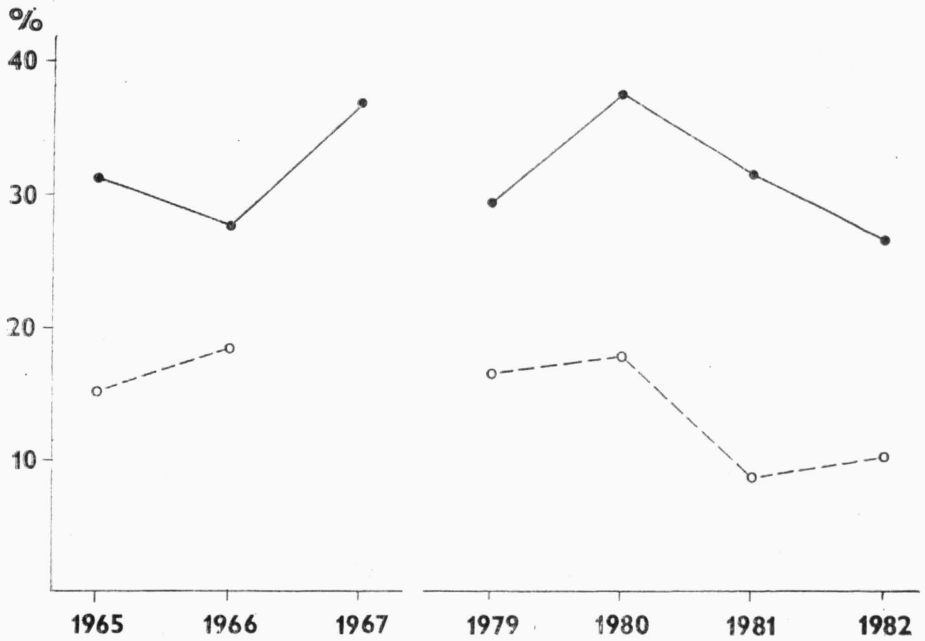


Fig. 2. — Cover changes of *Festuca valesiaca* (incl. *F. rupicola*) and *Carex humilis* in different years. Percentage cover indicates the average from all four permanent quadrats. Full line: *Festuca valesiaca*, dashed line: *Carex humilis*.

conditions in some years during the latter period. (The no. 4 quadrat is located in the lowest part of our transect, under more mesic conditions.)

Festuca valesiaca is the strong edificator in this stand, exhibiting the strongest competitive effort, here. It seems that the habitat conditions for this species are very suitable, here, and relatively unsuitable for the other potential competitors, above all for *Festuca rupicola*. Competitive superiority of *F. valesiaca* in this community seems to be confirmed by a contemporary experiment in which *F. valesiaca* was picked out on one plot and *Carex humilis* on the other one, and observation were made of the cover changes of both species following this disturbation; so far, the experiment has not been finished.

Festuca valesiaca tussocks are distributed fairly regularly, as it was evaluated by R-test after Clark et Evans (1954): R = 1.45. This ±regular distribution is probably caused by the competition among particular tussocks in the underground space; new tussocks have a low probability to establish themselves, unless some of the present ones become weaker or extinct. Thus, this spatial distribution is controlled by relations between mature tussocks of this species; only few seedlings can survive to mature stage. These circumstances limit the final number of all tussocks in the population.

Fig. 1. — Distribution of *Festuca valesiaca*, *F. rupicola* and *Carex humilis* on four permanent quadrats in a steppe community on the Strážiště Hill in 1965 and 1982. a = *Festuca valesiaca*, b = *F. rupicola*, c = *Carex humilis*.

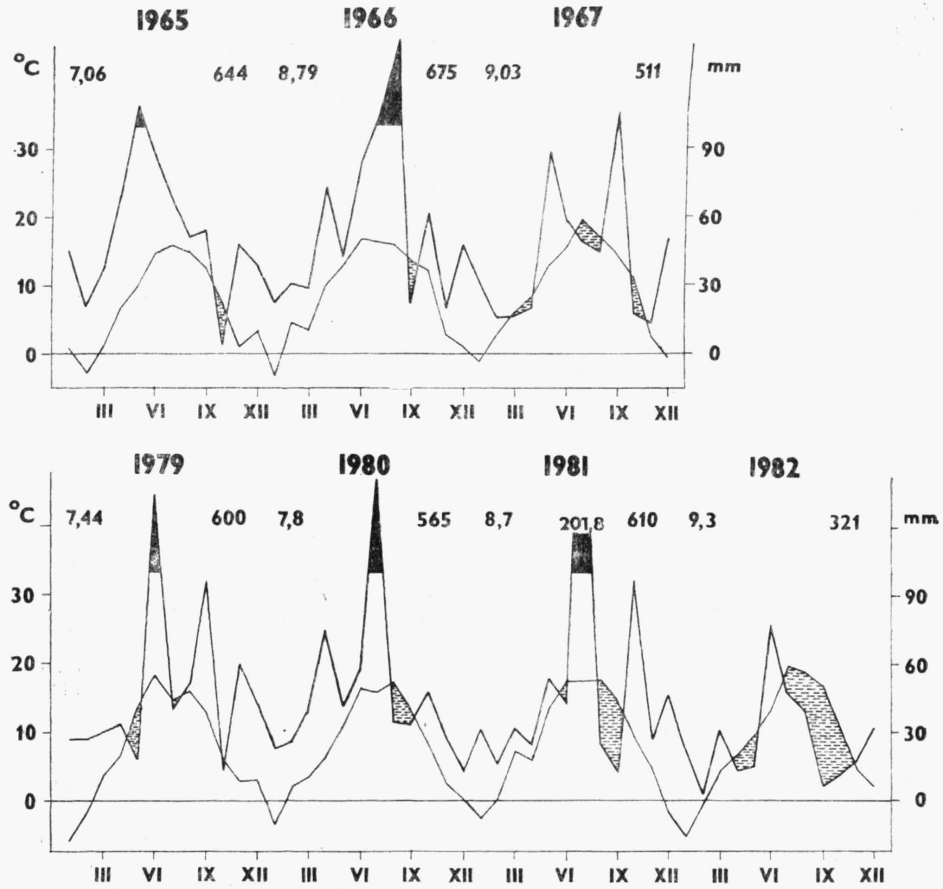


Fig. 3. — Annual fluctuations of precipitations and temperature according to data from climatic station Beroun (in 1979 from Praha-Ruzyně). Thin line: monthly averages of temperature, thick line: monthly totals of precipitation. Black area: wet period, dashed area: dry period.

Carex humilis, the co-dominant species, fills up, together with other species, the vacant place among or around *Festuca* tussocks. It is remarkable that after removing *Festuca valesiaca*, *Carex humilis* increased in its cover more than two times after three years.

Annual fluctuations of the precipitation and monthly means of temperature during 1965 to 1967 and 1979 to 1982, and respective changes of the cover degree (as averages from all four permanent quadrats) of *Festuca* and *Carex humilis* are shown in Figs. 3 and 2. Weather during the spring months seems to have a great influence on the development of the both principal species: early spring affects namely *Carex humilis*, while (April) May to June period is decisive for *Festuca valesiaca*. The latter species seems to be enhanced by a cold period between April and June, with a sufficient amount of precipitation (see years 1967 and 1980). Wet and colder weather seems to promote the growth of a more mesophytic form in *Festuca valesiaca*, characterized

by less compact but larger tussocks with less grey leaves, in contrast to dense, compact but smaller tussocks developing under dry and warm weather conditions. In the vertical projection, evaluated by the micromaps, the former case resulted in higher cover values of *Festuca valesiaca*.

Lacking precipitations in spring clearly limited the cover values of both main species (see years 1981 and 1982). Dry and warm weather in July and August did not damage those species (e.g. in 1967). In the extremly dry year 1982, the population of *Carex humilis* outlasted better then that of *Festuca valesiaca*. However, the relationship between the cover of *Carex humilis* and weather fluctuations interfers with competitive relationships (see above). Generally, changes of the cover of dominant species are in connections with the annual climatic fluctuations and do not express any long-term directional changes. However, relations between the cover values and weather fluctuations are probably of much more complex nature and more delicate than it could be described here.

The repeated investigation of the permanent plots also enabled to estimate age of certain plants. According to earlier estimate (PUČELÍKOVÁ 1967), most of the mature tussocks of *Festuca valesiaca* were between 5 and 10 years old in 1965. At present, we can identify several of them and estimate their age about 25 years. The above mentioned tussock of *Festuca rupicola* was in 1965 at least 10 years old; apparently, the life-span of this tussock can be at least 27 years. It is evident that some specimens of the both *Festuca* species can survive over a long time. The age structure of our population of *Festuca valesiaca* shows a slow exchange of plant individuals, leading to small variability of spatial distribution of tussocks (see above) and slow changes of the entire population. At the same time, the *Festuca* population maintained a good vitality and great seed production. Consequently, the population of *Festuca valesiaca* on the Strážiště Hill seems to be at an optimum stage of its development.

CONCLUSIONS

The steppe community analysed in our paper exhibits a high degree of persistence (see REJMÁNEK 1979). It means, the community is able to maintain itself within acceptable ranges for a long time. The cover changes of species are relatively great year by year, especially in relation to the fluctuations of the weather conditions in the spring, but the number of specimens is highly constant. No directional changes are apparent comparing the situation in 1965—67 and 1979—82. We consider the steppe community on the Strážiště Hill, as well as simillar communities in the Bohemian Karst and in other xerothermic regions of Bohemia, to be stable, viz. persistent. They do not probably exhibit obvious directional (successional) changes, now, if they are not influenced by human activities. They can be considered as a "preclimax" or "edaphic climax" (see WHITTAKER 1974). From the viewpoint of ecology of dominant species, the community includes stable populations with maximum exploitation of habitat resources.

Acknowledgments

We thank doc. Ing. J. Jeník, CSc. and Dr. J. Kolbek, CSc. for their helpful comments.

SOUHRN

Stepní společenstvo ze svazu *Festucion valesiacae* Klika 1931 bylo sledováno pomocí trvalých ploch 1 × 1 m (metodou mikromap) v letech 1965—67 a 1979—82 na vrchu Strážiště (440 m n.m.) v Českém krasu. Z předložených výsledků je možné vyvodit následující závěry: Sledované stepní společenstvo vykazuje vysoký stupeň persistence, tzn., že je schopno setrvávat v daném stavu po dlouhou dobu. Výkyvy v pokryvnosti hlavních přítomných druhů (*Festuca valesiaca*, příp. *F. rupicola*, *Carex humilis*) jsou sice z roku na rok poměrně značné, celkový počet dospělých exemplářů a jejich rozložení jsou však vysoce konstantní. Výkyvy pokryvnosti jsou v úzkém vztahu k chodu počasí v jednotlivých letech, především v jarních měsících. Ze srovnání období 1965—67 a 1979—82 vyplynulo, že společenstvo nevykazuje žádné patrné jednosměrné (sukcesní) změny. Stejnou situaci můžeme předpokládat i u jiných obdobných porostů v Českém krasu, případně i v ostatních xerothermních oblastech Čech, pokud tato společenstva nejsou ovlivněna antropickými zásahy. Takové porosty je možné považovat za „edafický klimax". Z hlediska autekologie dominantních druhů zahrnuje sledované společenstvo stabilní populace s maximálním možným využitím dostupných zdrojů.

REFERENCES

Clark P. J. et Evans F. C. (1954): Distance to nearest neighbor as a measure of spatial relationships in populations. — Ecology, Durham, 35 : 445—453.

Hroudová-Pučelíková Z. (1972): A comparative study of the ecology of Festuca valesiaca Gaudin and Festuca rupicola Heuff. — Folia Geobot. Phytotax., Praha, 7 : 53—79.

Jeník J. (1969): Otázka stepí v Čechách a ve světě. — Zpr. Čs. Bot. Spol., Praha, 4 : 128—131.

Jeník J. et Rejmánek M. (1969): Interpretation of direct solar irradiation in ecology. — Arch. Mat. Geoph. Biokl., Wien, ser. B, 17 : 413—428.

Ložek V. (1971): K otázce stepí ve střední Evropě. — Zpr. Čs. Bot. Spol., Praha, 6 : 226—232.

Martinovský J. O. et Kolbek J. (1984): Zum Begriff der Waldsteppe in Ost- und Mitteleuropa. — Preslia, Praha, 56 : 329—341.

Moravec J. (1970): Několik poznámek ke „stepní otázce" v Československu. — Zpr. Čs. Bot. Spol., Praha, 5 : 60—64.

Neuhäuslová Z. et Kolbek J. [red.] (1982): A list of higher plants, bryophytes and lichens of Central Europe used in the bank of geobotanical data in the Botanical Institute of Czechoslovak Academy of Sciences. — Průhonice.

Pučelíková Z. (1967): Ekologická studie kostřavy walisské (Festuca valesiaca Gaudin) a kostřavy žlábkovité (Festuca rupicola Heuff.). — Ms. [Dipl. Pr., depon in Knih. Kat. Bot. Přírod. Fak. UK, Praha]

Rambousková H. (1981): Water dynamics of some abandoned fields of the Bohemian Karst, Part 2: Plants. — Folia Geobot. Phytotax., Praha, 16 : 133—152.

Rejmánek M. (1979): Stability and complexity in biotic communities: Theoretical and empirical approach. — In: Ružička M. [red.]: Proc. 5th Intern. Symp. Probl. Ecol. Land. Res., p. 65 to 72. — Bratislava.

Slavíková J. [red.] (1982): Ecological and vegetational differentiation of a solitary conic hill (Oblík in České středohoří Mts.). — Praha.

Slavíková J. et al. (1984): Biologie druhu Festuca rupicola. — Zpr. Čs. Bot. Společ., Praha, 19, 1984, Mater. 4 : 1—9.

Smetánková M. (1959): Dry matter production and growth in lenght of overground part of Carex humilis Leyss. — Biol. Plant., Praha, 1 : 235—247.

Whittaker R. H. (1974): Climax concepts and recognition. — In: Knapp R. [ed.]: Vegetation dynamics, p. 139—154, The Hague.

Received 28 March, 1985