ACTA SOCIETATIS
BOTANICORUM POLONIAE
Vol. 49, nr 4: 493—506
1980

Competition between *Festuca rubra* L. and *F. pratensis* Huds. in natural conditions

MARIA WIDERA

Department of Ecology and Nature Protection, Institute of Botany,
Wrocław University, ul. Kanonia 6/8, 50-328 Wrocław, Poland

(Received: June 8, 1978)

Abstract

Analysis of the edaphic conditions and properties of pure and cenopopulations of *Festuca rubra* and *Festuca pratensis* allowed to establish the competitivity of these two species on 4 different lithological substrates in the Sudetes Foothills. A model of competition between *F. rubra* and *F. pratensis* was constructed on the basis of the biomass of their populations. On a substrate of porphyry, sand and granite *F. rubra* prevails in competition while on basalt *F. pratensis* is preponderant.

INTRODUCTION

A number of grassland plants, among them *Festuca pratensis* and *Festuca rubra* serve as object for model experiments. The latter are aimed at establishing the best composition of meadow and pasture mixtures with the application of various agrotechnical practices such as fertilization and irrigation. Planned model experiments for investigation of the course of competition between various cereal and grass species were undertaken (Wit et al., 1960; Bergh, Elberse, 1962). They devised models of competition for pairs of species in experimental conditions by sowing mixtures of two species next to their monocultures. The competition between various species in natural conditions has been less frequently studied, although numerous investigators, Sukatshev (1953), stress that the competition in natural conditions may be different than in experimental ones. According to Rademacher (1959), a condition for studying competition in natural associations is the occurrence of these species in almost pure populations next to their cenopopulations. The course of competition between *Hieracium pilosella* and *Festuca ru-*

bra (W i d e r a, 1978), it was found that investigations on competition can be studied between *Festuca rubra* and *Festuca pratensis* in natural conditions.

METHODS

In choosing the sites with *Festuca rubra* and *F. pratensis* the criterion was the abundant occurrence of both species, which would ensure a free choice of the experimental plots. In view of the different ecological amplitude of the species under study (H e g i, 1935), it was not easy to find a large number of sites on different lithological substrates. Therefore, the studies on competition between these species were conducted on 4 sites where, in agreement with R a d e m a c h e r's recommendation (1959), pure populations of *F. rubra* and *F. pratensis* grew next to their cenopopulations. They are components of a community which was classified as sward of the class *Sedo-Scleranthеretea* (S c a m o n i, 1967). A list of the localities where the sites with both species were chosen is given in Table 2. Within each site three 0.25 m^2 plots were marked out with pure *F. rubra* and *F. pratensis* populations and 6 plots with cenopopulations of these species of various abundance. A total of 48 experimental plots was chosen. From each site 4 soil samples from a depth of 5-15 cm were analysed:

1 — the current pH in water — potentiometrically;

2 — total nitrogen content — according to Kjeldahl (L i t y ń s k i et al., 1962);

3 — assimilable phosphorus, potassium, calcium and magnesium contents in Morgan solutions (N o w o s i e l s k i, 1968). Phosphorus by the molybdate method (N o w o s i e l s k i, 1968), potassium — photometrically by the modified method of Jonson-Ulrich (N o w o s i e l s k i, 1968) and calcium and magnesium by the complex method of B a r r o u s and S i m p s o n (1962). The Ca:Mg and K:Mg ratios were calculated.

Plants were examined for the following traits:

1 — density expressed by the number of tufts of *F. rubra* and *F. pratensis* on the given plot;

2 — the current state of *F. rubra* and *F. pratensis* populations biomass per surface unit area of 0.25 m^2, expressed as dry mass;

3 — maximal height of *F. rubra* and *F. pratensis tufts* (without inflorescences);

4 — length of longest roots of *F. rubra* and *F. pratensis*.

For statistical purposes mean values of the measured traits were taken. These parametres for pure *F. rubra* and *F. pratensis* populations were compared with the values for their cenopopulations.

Table 1

Frequency of occurrence of *Festuca rubra* and *Festuca pratensis* and of accompanying species on the studied sites

No	Species	Site no.	Frequency
1	*Festuca rubra* L.	36	100
2	*Festuca pratensis* Huds.	36	100
3	*Festuca ovina* L.	18	50
4	*Achillea millefolium* L.	12	33.3
5	*Holcus mollis* L.	10	27.8
6	*Poa annua* L.	10	27.8
7	*Trifolium dubium* Sibth.	8	22.2
8	*Luzula nemorosa* (Poll.) E. Mey.	7	19.4
9	*Stellaria media* Vill.	5	13.9
10	*Plantago lanceolata* L.	4	11.1
11	*Rumex acetosa* L.	4	11.1
12	*Melandrium album* (Hill.) Gercke	2	5.6
13	*Fragaria vesca* L.	1	3.3
14	*Potentilla argentea* L.	1	3.3
15	*Euphorbia cyparissias* L.	1	3.3
16	*Ceratodon purpureus* Brid.	10	27.8
17	*Hypnum cupressiformae var. lacunosum* Brid.	5	13.9
18	*Rhacomitrium canescens* Brid.	1	3.3

The results were subjected to statistical-mathematical elaboration comprising:

1 — analysis of one-way variance according to Permanent Stable Model I (Elandt, 1964) for establishing variability of elements content in soil and *F. rubra* and *F. pratensis* populations; the significance of differences was determined by Snedecor's F test at probability level 0.05 (Scheffe, 1959);

2 — simple and multiple correlations between the biomass values and between the relative biomass increment indexes of populations and the chemical characteristics of the soil; regression coefficients b_o, $b_1 \ldots b_n$ were calculated by the least-squares method according to the algorithm of Beale et al. (1967), and the coefficients of linear correlation were determined; significance tests were performed after Rao (1965).

RESULTS

CHARACTERISTIC OF EDAPHIC CONDITIONS

The chemical properties of the soil forms sites with *Festuca rubra* and *F. pratensis* are shown in Table 2. These soils exhibit acid pH, and differ from one another with pH values with the exception of those from sites 1 and 3.

Table 2

Chemical properties of soil on sites with *Festuca rubra* and *Festuca pratensis*

No	Site	Substrate	pH in water	Total N	Assimilable forms				Ca: Mg	K: Mg
					P	K	Ca	Mg		
					mg/100 g d. wt soil					
1	Rogoźnica	granite	4.4 b	543.1 b	0.40 a	14.05 b	75.45 b	77.34 b	0.98	0.18
2	Pomocne	basalt	4.8 c	609.0 c	1.08 c	31.25 d	51.70 a	399.33 d	0.13	0.08
3	Jordanów	sand	4.5 b	134.6 a	0.60 b	7.50 a	43.33 a	1.83 a	23.68	4.10
4	Sędziszowa	porphyry	5.2 d	156.8 a	1.07 c	25.00 c	130.55 c	98.66 c	1.32	0.25
LSD			0.27	41.33	0.05	1.54	15.45	7.2		
Snedecor's test	F estimated		19.34	393.7	411.1	512.4	68.8	6252.0		
	F tabular		4.07	4.07	4.07	4.07	4.07	4.07		

LSD — least significant difference.
The letters indicate the non significant differing volumes.

The content of assimilable forms of particular nutrient elements (Table 2) differed in the soils investigated. Especially poor was the sandy soil of the site 3 and the richest were those of sites 2 and 4. Especially great differences among soils occurred in Mg content (218×), whereas they were rather small with P (2.7×).

The Ca:Mg and K:Mg ratios were highest in soil on sand substrate (site 3) and lowest in soil on basalt substrate (site 2).

POPULATION CHARACTERISTIC

The characteristics of pure *F. rubra* and *F. pratensis* populations are listed in Table 3. The highest pure *F. rubra* population density was noted on sand substrate (site 3) and the lowest on basalt substrate (site 2). The highest biomass of pure *F. rubra* populations was found on site 3 and the lowest on site 2. The highest tussocks are characteristic for pure *F. rubra* populations from granite substrate (site 1) and lowest from basalt substrate (site 2). The longest roots were found in the pure *F. rubra* population on granite substrate (site 1) and the shortest on porphyry substrate (site 4).

The highest population density of pure *F. pratensis* was in contrast with *F. rubra* found on basalt substrate (site 2), and the lowest on sand substrate (site 3). The highest biomass of pure *F. pratensis* populations was found on basalt substrate (site 2) and lowest on sand substrate (site 3). The highest tussocks were noted in *F. pratensis* populations on basalt substrate and the lowest on granite. The longest roots were characteristic for pure *F. pratensis* populations from porphyry substrate (site 4) and the shortest on sand substrate (site 3).

CHARACTERISTIC OF CENOPOPULATIONS

The characteristic of *F. rubra* and *F. pratensis* populations are shown in Table 4. The highest density of *F. rubra* in the cenopopulations was noted on granite substrate (site 1) and the lowest on basalt (site 2). The highest tussocks of *F. rubra* grew in the cenopopulations on granite substrate (site 1) and the lowest on basalt (site 2). The longest roots of *F. rubra* were found in cenopopulations on granite substrate (site 1) and the shortest on porphyry substrate (site 4).

F. pratensis populations exhibited the highest density in cenopopulations on basalt substrate (site 2) and lowest on sand substrate (site 3). The highest biomass of this species was found in cenopopulations on basalt substrate (site 2) and the lowest on sand substrate (site 3). The highest tussocks are characteristic for basalt substrate and the lowest for granite substrate (site 1). The longest roots were noted on basalt substrate (site 2) and the shortest on granite (site 1).

Table 3

Characteristics of pure *Festuca rubra* and *Festuca pratensis* populations

Characteristics of populations		*Festuca rubra*				*Festuca pratensis*			
populations		density	biomass g	height of tussocks mm	length of roots mm	density	biomass g	height of tussocks mm	length of roots mm
1		77.7 ab	230.0 c	181.4 c	109.2 c	200 a	135.73 b	79.0 a	78.5 b
2		49.6 a	37.4 a	67.5 a	105.2 c	362 c	180.50 d	180.50 d	93.8 c
3		291.8 c	252.5 c	108.0 b	94.7 b	178 a	98.4 a	129.6 b	65.7 a
4		107.0 b	125.2 b	125.1 b	73.2 a	293 b	152.0 c	146.7 c	103.2 d
	LSD	41.48	23.78	22.28	10.02	43.46	16.11	16.92	7.84
Snedecor's test	F estimated	73.95	186.15	47.8	23.42	40.8	47.31	66.33	47.42
	F tabular	4.07	4.07	4.07	4.07	4.07	4.07	4.07	4.07

LSD — lest significant difference.
The letters indicate the non significant differing volumes.

Table 4

Characteristics of *Festuca rubra* and *Festuca pratensis* populations in cenopopulations

Characteristics of populations		*Festuca rubra*				*Festuca pratensis*			
populations		density	biomass g	height of tussocks mm	length of roots mm	density	biomass g	height of tussocks mm	length of roots mm
1		405.0 c	69.2 b	138.22 c	105.65 c	67.4 a	31.34 b	64.25 a	63.14 a
2		57.6 a	14.8 a	65.69 a	77.88 b	202.3 b	42.16 c	106.26 c	96.72 c
3		267.0 bc	88.45 c	99.80 b	59.04 a	58.80 a	22.45 a	81.45 b	73.81 b
4		195.9 ab	57.87 b	69.72 a	57.00 a	172.6 c	37.50 c	87.72 b	75.25 b
LSD		208.48	14.6	33.77	13.04	57.74	6.12	15.32	9.27
Snedecor's test	F estimated	4.85	48.52	10.33	31.99	17.09	20.17	13.64	24.49
	F tabular	4.07	4.07	4.07	4.07	4.07	4.07	4.07	4.07

LSD — lest significant difference.
The letters indicate the non significant differing volumes.

COMPETITION MODEL

The model of competition between *F. rubra* and *F. pratensis* was constructed on the same principle as that for competition between *Hieracium pilosella* and *Festuca rubra* (Widera, 1978). The model is based on the relation of the population biomass of both the competing species. It was assumed that *F. rubra* plants (r) surrounded by *F. pratensis* specimens (p) in cenopopulations occupy an area which is (k_{rp}) times larger than that occupied by *F. rubra* in pure populations. If we assume the value of the area occupied by pure *F. rubra* populations as 1, the coefficient of surface occupation for *F. rubra* in relation to *F. pratensis* in the cenopopulations (k_{rp}) will be:

$$k_{rp} = \frac{s_r}{s_p}$$

where s_r — relative contribution of *F. rubra* in cenopopulations,
s_p — relative contribution of *F. pratensis* in cenopopulations.

The proportion of the surface occupied by *F. rubra* in the cenopopulation to the total surface area is:

$$A_r = \frac{k_{rp} \cdot s_r}{k_{rp} \cdot s_r + s_p}$$

while the proportion of the surface occupied by *F. pratensis* in the same cenopopulation to the total surface area is:

$$A_p = \frac{s_p}{k_{rp} \cdot s_r + s_p}$$

When the biomass increment of the population of one species is proportional to the relative surface occupied, then the biomass increase in the cenopopulation will be:

$$O_r = A_r \cdot M_r = \frac{k_{rp} \cdot s_r}{k_{rp} \cdot s_r + s_p} \cdot M_r \quad (\textit{Festuca rubra})$$

$$(1)$$

$$O_p = A_p \cdot M_p = \frac{s_p}{k_{rp} \cdot s_r + s_p} \cdot M_p \quad (\textit{Festuca pratensis})$$

where M_r and M_p — biomass of pure *Festuca rubra* and *Festuca pratensis* populations, respectively. The relative coefficient of biomass increment of *F. rubra* in relation to that of *F. pratensis* (α_{rp}) is equal to the ratio of the biomass increment coefficients of the *F. rubra* and *F. pratensis* populations. On the basis of formula (1) this may be expressed as:

$$\alpha_{rp} = \frac{O_r/Z_r}{O_p/Z_p} = k_{rp} \cdot \frac{M_r}{M_p} \qquad (2)$$

where Z_r — biomass of *F. rubra* in cenopopulation,
Z_p — biomass of *F. pratensis* in cenopopulation.

The relative contribution of *F. rubra* to the cenopopulation is higher when α_{rp} is larger than 1 and it is smaller when α_{rp} is smaller than 1. The ratio of *F. rubra* population biomass increment to that of *F. pratensis* can be calculated in their cenopopulations with the use of formula (1) theoretical values.

The value of this ratio is positively correlated with that of the ratio of biomass of the *F. rubra* population to that of *F. pratensis* in the same cenopopulations (measured values). This relation is expressed by the following equation of linear regression:

$$O_r/O_p = 5.2249 + 4.522 \cdot Z_r/Z_p \qquad (3)$$

Formula (3) in the basic model of competition between *F. rubra* and *F. pratensis* in the given ecological conditions. It was further assumed that the value of ratio of biomasses of *F. rubra* population to those of *F. pratensis* (Z_r/Z_p) in the cenopopulations studied changes in dependence on the content of the basic macroelements in the soil such as nitrogen, phosphorus, potassium, calcium and magnesium and the pH values. The studied correlations between the *F. rubra* population biomass to that of *F. pratensis* populations ratio and the value of the foregoing chemical soil features demonstrated that the value of this ratio is positively correlated with calcium in the soil as expressed by the following linear regression equation,

$$Z_r/Z_p = 0.0797 \cdot Ca - 2.0892, \qquad (4)$$

whereas the correlation between the relative index of biomass increment of the *F. rubra* population in relation to that of the *F. pratensis* population (α_{rp}) and the value of the soil characteristics investigated indicated that this index is correlated negatively with magnesium content in the soil, as expressed by the following linear regression equation:

$$\alpha_{rp} = 5.1366 - 0.0126 \ Mg.$$

Evaluation of the relative biomass increment index of the *F. rubra* population in reference to that of the *F. pratensis* population on the rock substrates examined (Table 5) showed that on porphyry, sand and granite substrate the species *Festuca rubra* prevails over *Festuca pratensis*. On the other hand, on basalt substrate the competition is won by *F. pratensis*. The edaphic conditions on this rock substrate do not favour abundant occurrence of *F. rubra*. The basic model of competition between *F. rubra* and *F. pratensis* (formula 3, Fig. 1) illustrates the course of this competition in natural conditions within the scope of the edaphic conditions tested (Table 2).

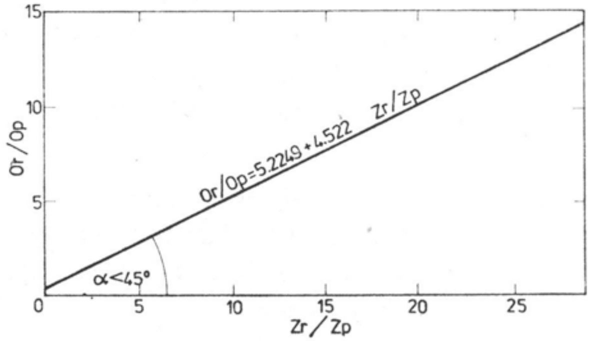

Fig. 1. Correlation between ratio of biomass increments of *F. rubra* and *F. pratensis* populations (O_r/O_p) and the ratio of biomasses of *F. rubra* and *F. pratensis* populations (Z_r/Z_p) in cenopopulations

Table 5

Relative index of biomass increment of *Festuca rubra* population in reference to that of *Festuca pratensis* population expressed as %

No	Substrate	$\alpha_{rp}>1$	$\alpha_{rp}<1$	Total
1	granite	64.3	35.7	100
2	basalt	—	100	100
3	sand	80	20	100
4	porphyry	100	—	100

DISCUSSION

Plant communities including *Festuca rubra* and *Festuca* pratensis are composed of few species (Table 1). This gives grounds to the high evaluation of the biotic potential of both competing species as compared with other accompanying species, in agreement with the rule of competitive exclusion (Smith, 1974).

The course of interspecific competition, beside other factors, is strongly influenced by edaphic conditions. According to MacArthur (1972) "every species has its own function of resource utilisation". Hegi (1935) reports that *F. rubra* has a wide ecological amplitude as regards edaphic conditions. It grows on acidic and arid light soil as well as on soils with pH close to neutral, fertile and heavy. On the other hand, *F. pratensis* thrives better on fertile soil with pH close to neutral. The present investigations indicate that *F. pratensis* exhibits the highest biomass productivity in pure and cenopopulations with *F. rubra* on basalt substrate, whereas *F. rubra* populations are most productive on a sand substrate (Tables 3, 4). The substrates on which both species grow do not show wide differences in pH. Thus, this reaction is not the reason of different biomass productivity of these species. Jusca et al., (1955) in experiments on the influence of fertilization on the competitivity of grasses demonstrated that high nitrogen fertilization changes the course of competition between *F. rubra* and *F. pratensis*. At low nitrogen content in the soils *F. rubra* dominates. On basalt substrate richest in nitrogen (Table 3) *F. rubra* shows the lowest biomass productivity and *F. pratensis* the highest, both in pure and in cenopopulations (Tables 3, 4). It may, therefore, be inferred that on nitrogen-rich soils *F. pratensis* populations have a higher competitivity which allows them to win the competition with *F. rubra*.

The occurrence of pure *F. rubra* and *F. pratensis* populations next to cenopopulations in natural conditions makes possible the construction of a model of competition between these species, as it was done for competition between *Hieracium pilosella* and *Festuca rubra* (Widera, 1978) and in experimental conditions by Wit et al. (1960), Bergh and Elberse (1962) and others.

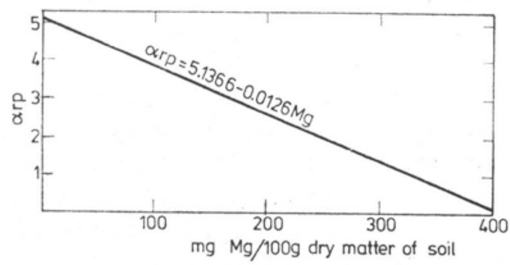

Fig. 2. Correlation between the relative biomass increment index for *F. rubra* in reference to that of *F. pratensis* populations (α_{rp}) and magnesium content in the soil

According to Paczoski (1951), the yield from a given surface unit is the function of the general nutritional conditions and competition for room. Therefore, the model of competition between *F. rubra* and *F. pratensis* was based on these parametres. Formula (1) illustrated the biomass increment of the populations of both competing species in cenopopulations. Formula (2) presents the relative index of biomass increment of the *F. rubra* population in reference to that of *F. pratensis*. The curve of the positive correlation between the ratio of biomass increment of both the populations (theoretical values) and the ratio of biomass of *F. rubra* to that of the *F. pratensis* population in cenopopulations (measured values) runs at an angle smaller than 45° (Fig. 1). According to Wit et al., (1960), this indicates a course of competition between these species, following model IV constructed by these authors for competition between *Lolium perenne* and *Trifolium repens*. This model can illustrate cases of competition when some factors limit the growth of one of the competing species. Such a restricting factor may be the level of indispensable nutrient component in the soil. In the competition between *F. rubra* and *F. pratensis* the magnesium level may be considered as such a factor. This is indicated by the negative correlation between the relative biomass increment index of *F. rubra* in relation to that of *F. pratensis* and the content of this element in the soil (Fig. 2). The lowest value of this index was noted when magnesium content in the soil was about 400 mg/100 g dry weight on basalt substrate (Tables 1, 5). This means that on this substrate the competitivity of *F. rubra* is lowest in relation to *F. pratensis,* and under such conditions, *F. pratensis* will win the competition, although on other substrates *F. rubra* will be dominant (Table 5). On porphyry substrate *F. rubra* exhibits the highest competitivity. In all cases the calculated values of this index α_{rp} are higher for this substrate than unity (Table 5). S a r o s i e k and W i d e r a (1978), when evaluating ecologically the *Festuca rubra* sites noted an influence of magnesium on the growth of plants of this species. Calcium seems to have a positive effect on the competitivity of *F. rubra.* This may be concluded from the positive correlation between the biomass ratio of *F. rubra* and *F. pratensis* populations, observed in the present studies and the content of this element in the soil (Fig. 3). In investigations on competition between *Hieracium pilosella* and *Festuca rubra* higher biomass values were found for the former when calcium content was higher in the soil (W i d e r a, 1978). Noteworthy is the highest content of this element in the soil on porphyry substrate, for which the calculated values of index α_{rp} indicate a dominance of the *F. rubra* population over *F. pratensis* (Tables 2, 5).

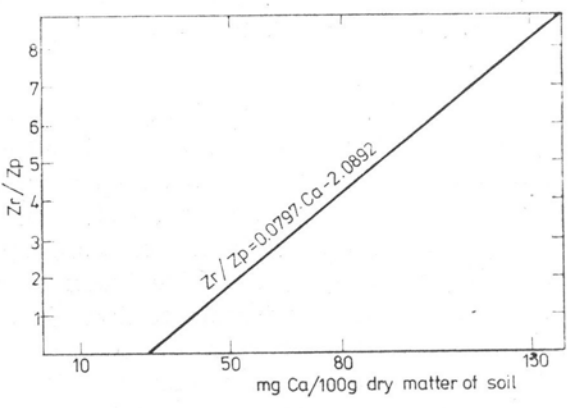

Fig. 3. Correlation between ratio of biomasses of *F. rubra* to *F. pratensis* populations (Z_r/Z_p) and calcium content in the soil

The edaphic conditions not only determine the amplitude of species occurrence, they also influence the group and individual properties of the competing plants. On the example of pure populations the influence of the substrate and the edaphic conditions associated with it on the

F. rubra and *F. pratensis* populations can be followed. In investigations on the ecological evaluation of *F. rubra* sites Sarosiek and Widera (1978) established that the height of the tufts and the length of roots of *F. rubra* plants in pure populations is positively correlated with the phosphorus content in the soil. It results from these studies that *F. rubra* plants form the largest tuft and have the longest roots on granite substrate, whereas *F. pratensis* plants develop best on basalt substrate (Tables 3, 4). The dependence of the abundance of the *Scabiosa columbaria* population on the character of the lithological substrate is pointed out by Rorison (1960).

In the present investigations is was found that the lowest density of *F. rubra* occurred in pure and cenopopulations on basalt substrate on which the density of *F. pratensis* is highest (Tables 3, 4). In cenopopulations of both *F. rubra* and *F. pratensis* the growth of tussocks and roots of both species is weaker than in pure populations. Both the species suffer losses owing to competition. This corresponds to the views expressed by Paczoski (1951) that "certain phenomena in the process of competition are universal and specific. For instance the mutual influence of plants if they grow in sufficient density. The weaker ones suffer more or even die, but for the stronger ones which win the competition this struggle does not pass without trace even when it is hardly noticeable. Under the influence of competition a certain specific collective group is formed in which the individuals are unequally developed presenting various stages of stifling. The highest degree of stifling causes the given individual to die prematurely, the next stage is a lack of flowering, a still weaker degree is flowering without fructification. These stages may be found in any excessively dense population. They are indices of competition".

The widest differences in the height of the *F. rubra* tussocks between pure and cenopopulations were observed on porphyry substrate on which this species exhibits the highest competitivity. On the other hand, in *F. pratensis* the widest differences in the hight of the tussocks were found on basalt substrate on which this species shows the highest competitivity in relation to *F. rubra*. It would seem, therefore, that on porphyry and basalt substrate the struggle is most unrelenting and it is *F. rubra* that wins on porphyry substrate, whereas on basalt the victory belongs to *F. pratensis*.

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Konkurencja między Festuca rubra L. i Festuca pratensis Huds. w warunkach naturalnych

Streszczenie

W oparciu o analizę warunków edaficznych i właściwości populacji czystych i cenopopulacji *Festuca rubra* i *Festuca pratensis* określono zdolność konkurencyjną obu gatunków na 4 różnych podłożach litologicznych w rejonie Pogórza Sudeckiego. Zbudowano model konkurencji między *Festuca rubra* i *Festuca pratensis* na podstawie relacji biomasy ich populacji. Na podłożu porfirów, piasków i granitów przewagę w konkurencji uzyskuje *Festuca rubra,* a na podłożu bazaltów — *Festuca pratensis.*