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Biomass production and size structure of *Calamagrostis villosa* populations in different habitats

Produkce biomasy a velikostní struktura populací *Calamagrostis villosa* na různých stanovištích

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Biomass production and size structure of the *Calamagrostis villosa* populations were studied in three habitats (forest, clearing, and bare spot) in the Krušné hory Mts. The forest population differs from both the others in all production characteristics measured, having lower biomass and higher living biomass /litter and root/ shoot ratios. No significant differences were ascertained between the clearing and the bare spot. Both the density and percentage of flowering tillers were the highest in the clearing population, whereas the highest total tiller density was found in the bare spot. The size of the individual tiller shows a great variation both among- and within-habitats. Variation in the tiller characters and the skewness of tiller weight distribution increase with density. Light is a factor decisive for differences in production and structure of the studied populations of *Calamagrostis villosa*.

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INTRODUCTION

Although there is a continued discussion on natural causes of forest decline in various parts of the world (Mueller—Dombois 1988), the industrial pollution has been implicated as the major cause of this phenomenon in Central Europe (Rebele 1987, Nilsson et Duinker 1987, Novák et Míchal 1989, Zachar 1989, Krause 1989, Pitelka et Raynal 1989 and others). Location of the Krušné hory Mts. within the North Bohemian mountain range makes them exposed to the effects of air pollution from the industrialized regions of Central and Western Europe (Jeník et Štursa 1987, for data on air pollution see Vavroušek et Moldan 1989). Moreover, poor forest management is also considered to contribute to forest decline (Pitelka et Raynal 1989).

Despite of efforts involving the revegetation of deforested sites in the Krušné hory Mts. (Peřina et al. 1984), there are vast areas overgrown by *Calamagrostis villosa* (Chaix) J. F. Gmel., an invasive grass species. It is a rhizomatous perennial forming extensive clones of shoots which die off every year. Spreading of the species has been mainly attributed to the light requirements met in the deforested sites (Samek 1988, Jakrlová 1989) as well as to the high production of both underground and aboveground biomass (Fiedler et Höhner 1987, Fiala 1989, Fiala, Jakrlová et Zelená 1989).

Calamagrostis villosa is distributed in the sub-oceanic zone of Europe (Rothmaler 1986). Naturally it occurs in the climax spruce forests (as. *Calamagrostio villosae-Piceetum*) as an important species of the herb layer (Moravec et al. 1983).

Occurrence of *C. villosa* remarkably reduces species diversity of invaded habitats (Pyšek 1990) and makes difficult the replantation of Norway spruce in the deforested areas affected by air pollution. On the other hand, the species may play a positive role in nutrient cycling and in the prevention of erosion. Although the ecological importance of *C. villosa* is well understood and stressed in literature (Samek 1988, Fiala, Jakrlová et Zelená 1989, Jakrlová 1989), the data published so far concern mostly quantitative estimation of the productivity. More data on biology and ecology of the species are thus needed.

This paper addresses the following questions: (1) What is the effect of habitat conditions on selected characteristics of the population? and (2) Are the changes in production linked with the changes in the size structure of the population?

STUDY AREA AND METHODS

The study area was situated in the Krušné hory Mts., a mountain range composed mostly of crystalline schists and reaching an altitude of over 1200 m a.s.l. The area belongs to the moderately cold climatic district, with mean annual temperature of 5.0 °C and precipitation of 984 mm per year (the Fláje meteorological station, 50-years average 1901—50) (Bárta et al. 1973). The units of reconstructed natural vegetation are represented by beech forests and waterlogged spruce forests (Mikyška et al. 1972). The study site was located at the westernmost shore of the Fláje reservoir (district of Litvínov, North Bohemia, 50.36 N, 13.17 E), at the altitude of 840 m a.s.l.

The research was carried out in three different habitat types, further referred to as follows: 1. Forest (F). This habitat represented the remainder of the climax spruce forest *Calamagrostio villosae-Piceetum.* The population of *C. villosa* was sampled from the proximity of trunks where the cover of Norway spruce canopy reached approximately 70 %.—2. Clearing (C). This habitat was a canopy gap of about 10×15 m situated within the foregoing forest.—3. Bare spot (B). This designation is used for the site deforested due to air pollution which was located in the vicinity of the forest.

The mutual proximity of sites was intentional in order to minimize the among-habitat differences in relief, soil conditions and climate. All investigated habitats were covered by monospecific stands of *C. villosa.*

Sampling was conducted on 8 August 1989. Six plots of 0.2×0.2 m were located randomly at each habitat and harvested for aboveground biomass estimation. Living biomass and litter were separated. Total underground biomass was determined using soil monoliths (45 mm in diameter, 200 mm in depth) which were taken in each of the sampling plots. The samples were washed in sieves of 0.5 mm mesh size (Chapman 1986, Fiala 1989). Plant material was dried at 85 °C for 48 hrs (Chapman 1986).

Individual shoot (tiller) was considered the modular unit convenient for the purpose of this study. Three out of the previous six plots sampled in each habitat were further analysed. The following data were recorded for each tiller present: height (measured as a distance from the base to the tip of the latest blade), number of leaves, total tiller biomass, and biomass of the culm, blades, and panicle (in flowering tillers). The estimation of leaf area index was based on the leaf weight (Jakrlová 1987).

Twenty more plots of 0.2×0.2 m were located at random in each habitat in order to obtain data on total tiller density and density of flowering (reproductive) tillers.

Table 1. – Production characteristics of the *Calamagrostis villosa* stands in different habitats. Means ± standard deviations are shown. Row values followed by the same letter are significantly different in Man-Whitney U test ($P < 0.05$)

	forest	clearing	bare spot	n
aboveground biomass (gm^{-2})				
– total	245.3 ± 39.3^{ab}	1188.1 ± 107.0^{a}	1227.8 ± 111.8^{b}	6
– living	108.0 ± 9.4^{ab}	323.1 ± 86.9^{a}	350.3 ± 56.4^{b}	6
– litter	137.3 ± 32.0^{ab}	865.0 ± 67.7^{a}	870.4 ± 90.7^{b}	6
total underground biomass (gm^{-2})	1295.0 ± 374.1^{ab}	2148.8 ± 506.5^{a}	2594.6 ± 313.4^{b}	6
total plant biomass (gm^{-2})	1539.5 ± 381.4^{ab}	3376.5 ± 556.4^{a}	3870.1 ± 281.7^{b}	6
underground/total aboveground biomass	5.35 ± 1.66^{ab}	1.82 ± 0.44^{a}	2.18 ± 0.35^{b}	6
living biomass/litter ratio	0.81 ± 0.17^{ab}	0.37 ± 0.10^{a}	0.40 ± 0.09^{b}	6
total density (tillers.m^{-2})	753.8 ± 269.7^{ab}	1924.7 ± 446.6^{ac}	2881.7 ± 851.3^{bc}	20
density of flowering tillers (m^{-2})	25.4 ± 25.7^{ab}	364.6 ± 276.7^{ac}	95.2 ± 148.5^{bc}	20
percentage of flowering tillers (%)	9.9 ± 4.1^{a}	19.1 ± 13.1^{ac}	3.1 ± 4.1^{c}	20
proportion of biomass in blades (%)	0.57 ± 0.0	0.37 ± 0.10	0.37 ± 0.03	3
specific leaf area (cm^2g^{-1})	427.9	412.4	236.9	1
LAI	2.71	3.42	3.30	1

Production characteristics were used according to Květ et al. (1971). Non-parametric Mann-Whitney U test (Sokal et Rohlf 1981, Prince 1986) was used to evaluate differences among- and within-habitats. Variation in the tiller characters was measured using the coefficient of variation C.V. Asymmetry of the size frequency distribution was measured using the skew g_1 (Sokal et Rohlf 1981, Hutchings 1986, Hara 1988).

RESULTS

The forest population differed significantly ($P < 0.05$) from both clearing and bare spot ones in all the production characteristics investigated (Table 1). It had lower total aboveground biomass (about 80 % smaller), living aboveground biomass (70 %), litter (85 %), and the total underground biomass (40—50 %). The living biomass/litter ratio was approximately doubled in the forest habitat which is caused by the low amount of litter recorded in this habitat. No significant differences in the production characteristics were ascertained between the clearing and the bare spot.

Total tiller density of 2881.m^{-2} was recorded in the bare spot. This value was about 50 % higher than that found in the clearing (1924.m^{-2}). The forest population showed the lowest tiller density of 734.m^{-2}. The differences were all significant ($P < 0.05$).

Both the density and the percentage of flowering tillers were highest in the clearing population. When the forest was compared with the bare spot, significantly lower density of flowering tillers was found in the former habitat.

Table 2. – Tiller performance in the plots sampled (0.2 × 0.2m). Means ± standard deviations are shown. Column values followed by the same letter are significantly different in Man-Whitney U test ($P < 0.05$). Biomass is given in mg, height in cm.

habitat		forest	
plot no.	1	2	3
non-flowering tillers:			
n	46	35	45
height	35.3 ± 7.4	39.1 ± 8.5	40.5 ± 7.2
number of leaves	4.3 ± 0.8	4.3 ± 1.1	4.2 ± 0.8
total biomass	81 ± 32	104 ± 45	93 ± 39
culm biomass	35 ± 17	44 ± 21	40 ± 19
blade biomass	46 ± 17	60 ± 27	54 ± 21
flowering tillers:			
n	–	1	1
height		58	55
number of leaves		3.0	4.0
total biomass		116	183
culm biomass		70	103
blade biomass		33	56
panicle biomass		13	24

However, the percentage of reproductive tillers in the forest is not significantly different from the value recorded in the bare spot.

Tillering occurred only in the bare spot population (26.0 ± 8.9 % of the total number of shoots).

Leaf weight ratio (LWR) was conspicuously higher in the forest (0.57 compared to 0.37 in the other habitats). In spite of this, leaf area index (LAI) reached higher values in the clearing and the bare spot than in the forest (Table 1). The specific leaf area (SLA) was nearly the same in the forest and in the clearing (427.9 cm^2g^{-1} and 412.4 cm^2g^{-1}, respectively), whereas in the bare spot population it was about 45 % lower (236.9 cm^2g^{-1}).

Data on tiller characters are presented in Table 2. Regarding the tiller height and the number of leaves, no significant differences were found within the data set. Tiller sizes expressed as their total biomass were compared using the Mann-Whitney U test (Table 3). It is obvious that significant differences in the tiller size ($P < 0.05$) may be detected both among- and within-habitats. However, the number of significantly different results obtained was higher when the clearing or the bare spot were compared with the forest. On the other hand, the differences among the clearing and the bare spot populations were mostly non significant. This indicates an increase in the mean tiller biomass in both clearing and bare spot. Nevertheless, it is not possible to consider tiller size as a population characteristic distinguishing among habitats.

Differences in the tiller size may be ascribed mainly to the differences in the culm biomass whereas the biomass of blades did not vary so much.

The reproductive tillers were higher and had greater total biomass and culm

clearing			bare spot		
1	2	3	1	2	3
39	53	47	113	45	92
43.4 ± 9.3^{a}	64.4 ± 14.0^{a}	50.4 ± 10.0^{a}	40.7 ± 5.2	42.4 ± 11.5	41.6 ± 10.5^{a}
4.0 ± 0.8	3.7 ± 0.9	3.1 ± 0.8	3.4 ± 1.2	3.4 ± 1.7	3.8 ± 2.0
117 ± 56^{b}	219 ± 128^{b}	114 ± 55^{b}	114 ± 65	176 ± 132	192 ± 154^{b}
57 ± 40^{c}	133 ± 81^{c}	71 ± 37^{c}	79 ± 45	116 ± 89	120 ± 97^{c}
60 ± 32	86 ± 54	42 ± 27	55 ± 29	60 ± 48	72 ± 71
16	8	27	–	2	21
74.0 ± 7.9^{a}	96.8 ± 11.9^{a}	81.1 ± 12.2^{a}		106.5 ± 12.0	78.7 ± 22.5^{a}
3.8 ± 1.0	3.4 ± 0.5	3.3 ± 0.6		5.5 ± 0.7	4.3 ± 1.5
237 ± 68^{b}	430 ± 122^{b}	243 ± 113^{b}		747 ± 198	578 ± 240^{b}
153 ± 38^{c}	306 ± 73^{c}	176 ± 87^{c}		535 ± 146	392 ± 142^{c}
51 ± 23	83 ± 38	42 ± 17		113 ± 36	129 ± 80
32 ± 14	40 ± 17	25 ± 15		98 ± 16	53 ± 45

Tab. 3. – Differences in tiller biomass within habitats (indicated by bold-face types) and among habitats. * $P < 0.05$, NS – non-significant.

plot no.		forest 1	forest 2	forest 3	clearing 1	clearing 2	clearing 3	bare spot 1	bare spot 2	bare spot 3
meadow	1									
	2	*								
	3	**NS**	**NS**							
clearing	1	*	NS	*						
	2	*	*	*	*					
	3	*	NS	*	**NS**	*				
forest	1	*	NS	NS	NS	*	NS			
	2	*	*	*	NS	NS	NS	**NS**		
	3	*	*	*	*	NS	*	*	**NS**	

biomass than non flowering tillers sampled from the same plot. In all cases investigated (C 1, 2, 3, B 3), the differences were significant ($P < 0.05$).

Although the total density of tillers was lower in the clearing than in the bare spot, the total aboveground biomass was approximately the same in both habitats (1188 vs. 1228 gm^{-2}). This may be explained by higher proportion of reproductive tillers in the clearing that are approximately twice as heavy as the vegetative ones.

Variation in selected tiller characteristics is presented in Table 4. The highest values of the coefficient of variation were stated in the bare spot. The only

Tab. 4. – Variation of selected tiller characteristics compared for the habitats investigated. Mean values of the coefficient of variation (%) calculated from 3 plots are presented.

	Characteristic	Forest	Clearing	Bare spot
flowering tillers	height	20.1	21.0	21.7
	number of leaves	21.1	23.4	46.0
	total biomass	41.5	51.5	70.7
	culm biomass	47.9	61.1	71.5
	blade biomass	40.3	60.1	77.1
non-flowering tillers	height		16.3	28.3
	number of leaves		19.7	34.9
	total biomass		34.8	41.5
	culm biomass		32.7	36.2
	blade biomass		43.8	62.0
	panicle biomass		47.9	84.9

exception is the height of non-flowering tillers, showing relatively small variation in all the habitats studied. Generally, the parameters measurement of which is not linked with the biomass estimation (height, number of leaves) are less variable in both vegetative and reproductive tillers. A conclusion may be drawn that the variation in the tiller performance increases with density.

Frequency distribution of tiller weight is presented in Fig. 1. Asymmetric, positively skewed weight distributions are typical of all samples analysed with the only exception of F 2 which is close to normal distribution. Although there are remarkable within-habitat distinctions, generally low weight skewness may be observed in the forest population. The g_1 value is apparently higher in clearing and, especially, in the bare spot population even if the reproductive tillers which contribute to the increase of skewness are not taken into account. In general, the skewness clearly increases with tiller density (Fig. 2).

Most of the size distributions presented for clearing and bare spot populations show more or less obvious bimodality, being often stressed or even caused by reproductive tillers.

Frequency distributions of tiller height are presented on Fig. 1. The bimodality apparent in bare spot population clearly reflects a high number of flowering tillers. In comparison with the weight distribution, there is an obvious shift towards normally or even negatively skewed distribution in all the habitats investigated.

DISCUSSION

The data available so far on the biomass production of *C. villosa* show conspicuous differences according to the habitat conditions. Significantly higher total aboveground biomass, both living and dead, as well as the lower underground/aboveground biomass ratio was found in the flat site in comparison with the steep slope (FIALA, JAKRLOVÁ et ZELENÁ 1989). The total plant biomass estimated in deforested sites of the Moravian-Silesian Beskydy Mts. was 3580—3620 gm^{-2} (FIALA, JAKRLOVÁ et ZELENÁ l.c.) This is a value similar to those reported by the present paper (3376.5 gm^{-2} in the clearing and 3870. 1 gm^{-2} in the bare spot, respectively). The average shoot density in the flat site studied by FIALA, JAKRLOVÁ et ZELENÁ (l.c.) was about 30 % higher (3810 m^{-2} on average, n=10) than that recorded in the meadow site of this study (2882 m^{-2}). However, the maximum value of shoot density stated in the Krušné hory Mts. reached 4000 shoots.m^{-2}. Shoot densities recorded in the Orlické hory Mts. (PAPÁČKOVÁ in lit.) are in accordance with the results of this study as well (maximum values of 750—925 m^{-2} in the shaded forest site and 3900 m^{-2} in the deforested site, respectively). The aboveground living biomass is similar in all the regions compared (323.1—350.3 gm^{-2} in the Krušné hory Mts., 289—355 gm^{-2} in the Beskydy Mts., and approximately 400 gm^{-2} in the Orlické hory Mts.)

The extent of belowground versus aboveground biomass appears to be a function of a factor which is more limiting to production (CODY 1986). Above or belowground stresses thus change root/shoot partitioning in favour of the affected part of the plant (HUNT 1988). Moreover, nutrient availability, plant age and the other factors may be also involved in changing the root/shoot ratio. Light becomes clearly a factor limiting productivity of *C. villosa* in the shaded forest habitats. However, availability of light in the herb layer dra-

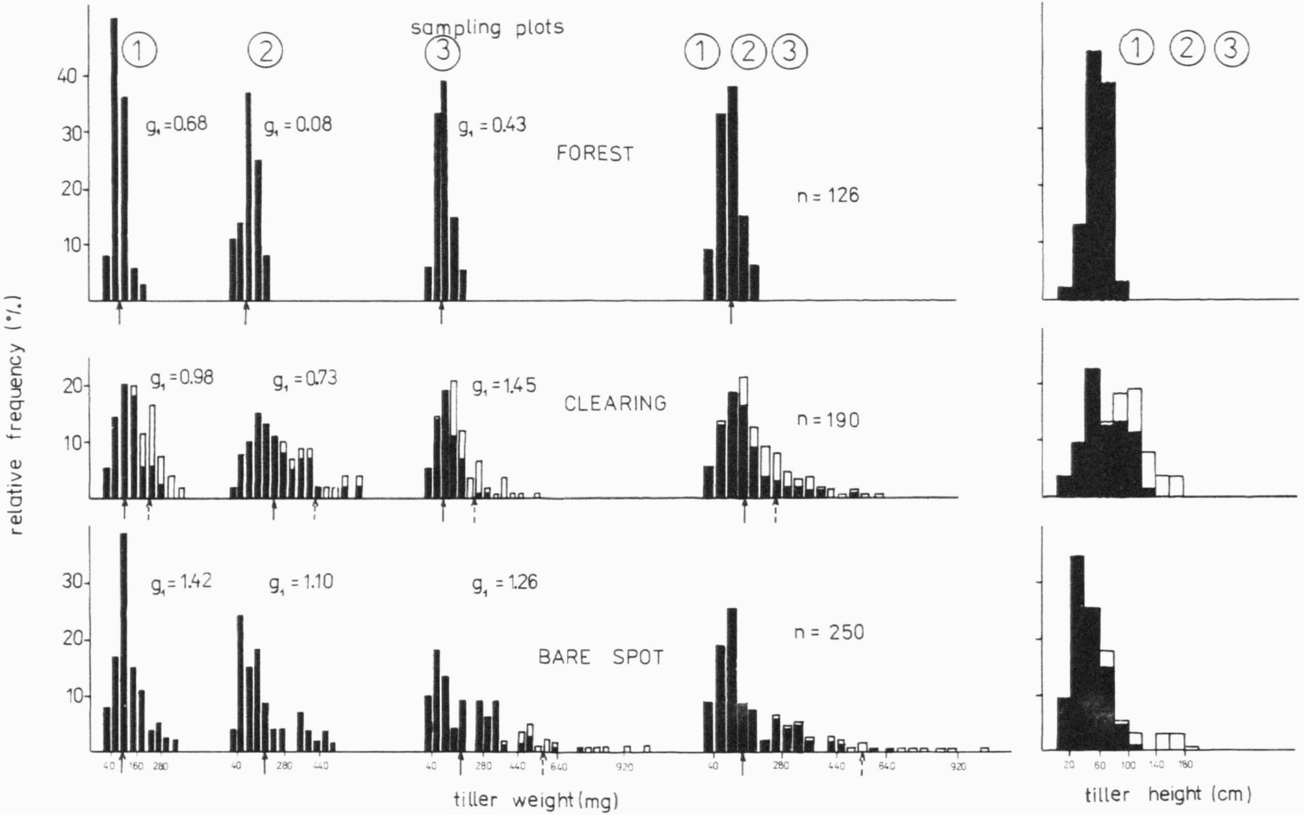

Fig. 1. — Frequency distributions of tiller weight in the habitats studied. The proportions of non--flowering (full bars) and flowering (empty bars) tillers are shown. Numbers of sampled plots corresponding to those presented in Table 2 are given in the circles. Values of skewness g_1 are shown for each plot. Height frequency distributions are added for comparison. The range of weight classes is 40 mg and that of height classes 20 cm, respectively.
Mean tiller sizes are indicated by arrows: ← (vegetative tillers only) ←--- (both vegetative and reproductive tillers included).

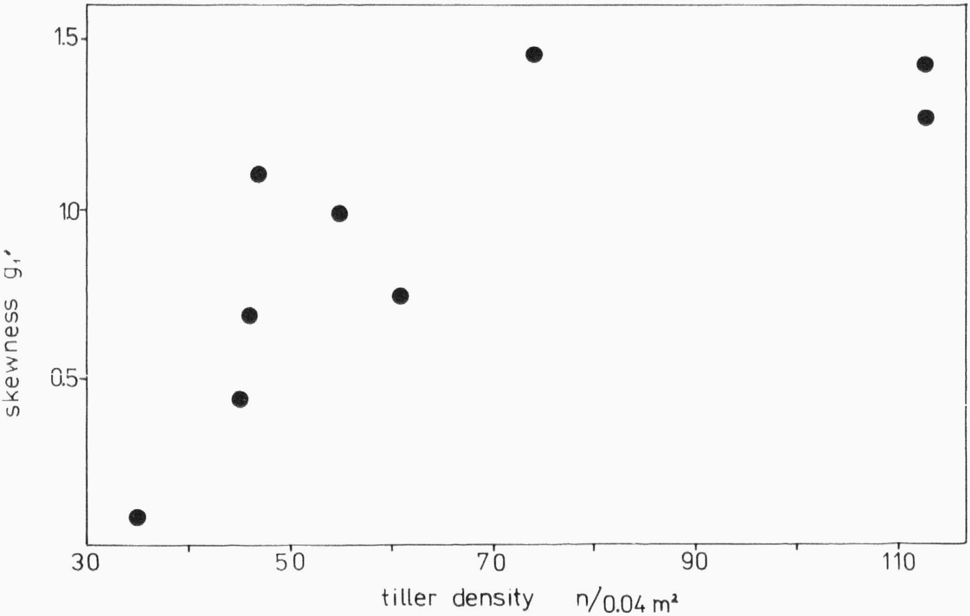

Fig. 2. — Skewness g_1 calculated from the weight distribution data plotted against tiller density.

matically increases after deforestation which leads to the more intense competition among individual tillers. This leads to the higher aboveground productivity and consequent decrease of the root/shoot ratio.

Tillering, the occurrence of which was recorded only in the bare spot population of *C. villosa*, is reduced by increased shading (Deregibus et al. 1985). High light intensity at the base of the plant promotes tillering as has been shown experimentally in several species of perennial grasses by Everson, Everson et Tainton (1988).

Among the four aspects of plant population structure (Hutchings 1986), the plant performance is stressed in this paper. Generally, many aspects of performance are correlated with size. An approach based on estimation of individual plant size provides more detail information about the structure of a population (Hara 1988).

The range in size of individual plants of the same age within a species can cover several orders of magnitude, especially in dense stands in which pronounced size hierarchies have developed (Jones 1985). In *C. villosa*, size inequality measured by the coefficient of variation reached 57—80 % in the bare spot population, density of which was the highest. There are reports that size inequality increases with density in most cases where competition is mainly for light (Weiner 1985 and Weiner et Thomas 1986 cited by Hara 1988). In closely spaced crops the coefficient of variation of plant size as high as 100—200 % and more has been reported (Benjamin et Hardwick 1986).

Within a mature population, individual plants have frequency distributions of weight that are asymmetric and positively skewed (Obeid et al. 1967, Ogden 1970, Harper 1977, Sarukhán, Martínez-Ramos et Piñero 1984, Watkinson

1985, HUTCHINGS 1986, BENJAMIN et HARDWICK 1986 and many others). Factors influential in promoting variation in the sizes of plants are (1) the size of seeds, (2) individual relative growth rate controlled by genotype, (3) time of emergence relative to neighbours, and (4) the size of space unoccupied by other members of a population (ROSS et HARPER 1972).

However, one must bear in mind that the tiller population of *C. villosa* does not represent a population of genetically independent individuals. Nevertheless, marked size hierarchies are developed among the members of a clone and the features of frequency distributions obtained correspond to those reported for the populations of individual plants. Most of the factors mentioned above are probably involved in promoting size hierarchy in the plant with such a clonal growth habit, too. Instead of seed size, the amount of reserves stored in rhizomes may play the respective role. Moreover, there is no information available on the intrapopulational genetic diversity of *C. villosa* which may be considerable within a clonal species in general (TURKINGTON et HARPER 1979, HARPER 1977, TURKINGTON 1985).

Although there are cautions to this rule (WATKINSON 1985), it is often argued that skewness increases not only with time but also with density (OBEID 1967, HUTCHINGS 1986, BENJAMIN et HARDWICK 1986). Results presented on Fig. 2 support this view at the level of a clonal plant.

Much variation in the individual plant weight may be caused by inter-plant competition (HUTCHINGS 1986). In the dense stands of *C. villosa*, a competition for light among tillers may be supposed. However, it is not possible to infer the extent of intraspecific competition within a population from the shape of the frequency distribution alone (WATKINSON 1985). Similarly the bimodality is considered to develop more usually in the circumstances where competition has taken place (FORD 1975). However, the sensitivity of its appearance to the number of classes in the histogram makes difficult to assess bimodality (HUTCHINGS 1986).

Differences found between the shaded population of *C. villosa* and those exposed to light allow to conclude that light conditions play an important role in the structural and productional differentiation within the species (Table 5).

Tab. 5. – Comparison of shaded population (F) with those exposed to light (C, B). Only population characters in which both groups differ are presented.

Characteristic	Forest (F)	Clearing (C), Bare spot (B)
biomass production	low	high
tiller density	low	high
flowering intensity	low	medium (B) – high (C)
root/shoot ratio	higher	lower
inequality of tiller size	lower	higher
skewness of the size frequency distribution	low	high
bimodality of the size frequency distribution	no	yes

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SOUHRN

Populace druhu *Calamagrostis villosa* (Chaix) J. F. Gmel. byly studovány na třech různých stanovištích v Krušných horách: v lese pod zápojem smrku, na pasece a na odlesněné imisní holině. Lesní populace se od obou zbývajících statisticky průkazně lišila nižší nadzemní (živou i stařinou) i podzemní biomasou, dále vyšším poměrem živé biomasy ku stařině a nadzemní biomasy ku podzemní. V lese byl zjištěn také vyšší podíl biomasy v čepelích (LWR) a nižší hodnota indexu listové plochy (LAI). Mezi populacemi na pasece a na holině nebyly zjištěny žádné statisticky průkazné rozdíly v produkci biomasy. Specifická listová plocha je nejnižší na holině (236,9 cm^{2}g^{-1}), zatímco na pasece a v lese dosahuje hodnot téměř dvojnásobných (412,4 a 427,9 cm^{2}g^{-1}).

Celková denzita stébel je nejvyšší na holině (průměrně 2 881,7 m^{-2}), na pasece dosahovala 1 924,7 a v lese 753,8 stébel/m^2. Denzita kvetoucích stébel byla naproti tomu nejvyšší na pasece (346,4 m^{-2}), na holině bylo zjištěno 95,2 a v lese 25,4 kvetoucích stébel/m^2. Jejich procento je nejvyšší na pasece; les a holina se v tomto ohledu neliší. Pouze u populace na holině bylo zaznamenáno odnožování (26,9 % stébel).

Biomasa jednotlivých sterilních stébel je velmi variabilní, průkazné rozdíly byly zjištěny jak mezi stanovišti, tak mezi plochami v rámci jednotlivých stanovišť. Ačkoliv existuje tendence k tvorbě mohutnějších stébel na pasece a holině, nelze považovat biomasu stébla za rozlišovací parametr mezi populacemi z různých stanovišť. Kvetoucí stébla se od sterilních v rámci populace liší větší výškou a biomasou.

Variabilita vlastností jednotlivých stébel měřená variačním koeficientem je nejvyšší u populace holiny a stoupá s denzitou. Pomocí vlastností frekvenční distribuce velikostí jednotlivých stébel lze odlišit lesní populaci od paseky a holiny. Šikmost rozdělení stoupá s celkovou denzitou stébel.

Ve většině sledovaných charakteristik se liší lesní zastíněná populace od dalších dvou, které jsou vystaveny více světlu; mezi těmi byly naopak zjištěny rozdíly pouze v celkové denzitě stébel, intenzitě kvetení a některých parametrech velikostní struktury (šikmost, bimodalita). Výsledky této práce lze tudíž považovat za potvrzení významu světelných podmínek pro biologii a ekologii druhu *Calamagrostis villosa.*

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