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Tiller demography of *Festuca rubra* in a mountain grassland: seasonal development, life span, and flowering

Demografie odnoží u *Festuca rubra* v horské louce: sezónní vývoj, délka života a kvetení

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The paper reports on demography of individual tillers in seventeen selected tussocks of *Festuca rubra* subsp. *rubra* over four vegetation seasons in a managed species-poor *Nardetalia* grassland. Natality of tillers peaked once a year only in spring; there was no increase of natality after the summer clipping. Tiller mortality showed no pronounced seasonal variation. Though flowering invariably resulted in the tiller death, flowering accounted only for 13-15% of the overall tiller mortality. Flowering tillers were statistically bigger already in the previous year, though the strength and timing of this size difference differed between years. Life span of tillers varied strongly, from several weeks to several years. Tiller survivorship was roughly exponential.

Introduction

Demography of grasses is one of the processes playing crucial role in grassland dynamics. Owing to several possible definitions of an individual in grasses, their demography may be studied at several hierarchical levels: (1) at the level of clones (genetic individuals, Eriksson 1993); (2) at the level of tussocks, i.e. the large life cycle of Russian authors (Gatsuk et al. 1980, Fowler 1984, Moloney 1988, Scheiner 1988); (3) at the level of tillers (Danais 1984, Garnier et Roy 1988, Kotanen et Jefferies 1987, Butler et Briske 1988, Bazely et Jefferies 1989, Jónsdóttir 1991); (4) at the level of leaves (Sydes 1984, Mitchley 1988). Each of these levels has its characteristic time scale; for the short term change in mown grasslands tiller demography is the most important process. There are numerous studies of tiller demography in experimental swards (see e.g. Langer 1963, Davies et Thomas 1983, Colvill et Marshall 1984); demography of grasses in natural communities is studied much less (cf. Jónsdóttir 1991). Therefore many processes, well known from experimental swards, are insufficiently documented in natural populations, e.g. life span of individual tillers, their mortality and natality rates over vegetation period, rate of flowering etc.

The present study reports on basic data on tiller demography in *Festuca rubra* subsp. *rubra*, a widespread hexaploid type from the *F. rubra* complex, in an extensively managed (mown) grassland. *F. rubra* grows here in a multispecies mountain grassland, where it forms loose tussocks partly mixed with other species. The study aims primarily to provide basic demographical data for comparison with other grass species and other grassland systems.

Methods

Study site

The data were collected in a mountain grassland in the Krkonoše Mts., NW part of the Czech Republic (Severka settlement, ca. 3 km NW of Pec pod Sněžkou, altitude approx. 1100 m above sea level). The vegetation period starts in about mid May when snow melts away (e.g. 10th May in 1988). Mean temperature in the warmest month (July) was 13.6°C (1988), 13.7°C (1989). The last month with average temperature above zero was October. The grasslands under study are managed in the traditional way, i.e. mowed once a year and grazed late in the autumn. They were manured once in several years. The studied grasslands are rather species poor, with only five important species: *Anthoxanthum alpinum, Deschampsia flexuosa, Festuca rubra, Nardus stricta* and *Polygonum bistorta*. These species always accounted together for 95% of the total living aboveground biomass. From the phytosociological point of view, the meadows are classified as *Sileno-Nardetum pleurozietosum (Nardo-Agrostion* alliance, *Nardetalia* order, see Krahulec 1990).

The small scale structure of the grassland is rather complex. In a 3 x 3 cm square, there are 1 to 6 species (average 2.1-2.8 depending on the site), density of *F. rubra* in the *F. rubra* occupied squares ranges from 1 to 20 (average 3.1-5.6; Krahulec et al., unpubl. data).

Data collection

Seventeen tussocks of *F. rubra* were selected for the study. All of them were located in an area of ca. 12 x 3 m. The tussocks were selected with an *a priori* requirement that (i) there be no *F. rubra* in their close surroundings (up to 10 cm) to prevent uncertainty in delimiting the tussocks in further measurements, and (ii) they have a workable number of tillers (less than 25 at the beginning).

Marking of tillers was done using coloured plastic rings (2-4 mm in diameter and 3-5 mm in length); to increase the number of combinations, the rings were marked with 0-4 notches. Each ring was cut vertically so that it could be opened and put on the grass tillers; the material was elastic enough to hold the ring on the tiller over the whole observation period. The ring was put on the tiller below the insertion of the lowest leaf blade. There were virtually no lost rings.

Because of this system of ring positioning, intravaginal daughter tillers appeared as a rule within the rings of their mother tillers; they were marked with their own rings, but they were left inside their mother rings until the surrounding leaf sheath of the mother tiller decomposed. Very small young daughter tillers were not marked; they were identified through their mother tillers. Though there was no separate experiment to test for adverse effects of rings on marked tillers, none were observed.

At each recording, each tiller was identified using its marking; its number of leaves and length of its longest leaf blade were recorded. These variables explain 62% of the variance in the tiller mass (Herben et al. 1993a). All green leaves were counted; partially green leaves were counted if the green part of the blade exceeded 10 mm (cf. also Sydes

1984); young developing leaves were counted if the length of the exserted part exceeded 10 mm. In July, fertile tillers were recorded separately and the length of the culm was measured. Mother tillers of newly appeared intravaginal tillers were recorded. Altogether 1251 tillers were observed.

The observation started in the spring 1987 and continued until the summer 1990. Three recordings were done before the mowing (period late May to mid July) and two to four recordings after the mowing (August - October). The first spring recording was done approximately ten to fourteen days after the snow had melted away; the last autumn recording was done as late as possible before the permanent snow cover. Exact dates of the recordings were: 1987: 4/6, 25/6, 14/7, 5/8, 29/8, 14/9, 10/11; 1988: 24/5, 23/6, 9/7, 3/8, 5/9, 12/10; 1989: 19/5, 15/6, 8/7, 7/9, 4/10; 1990: 10/5, 15/6, 10/7. Every year the tussocks were clipped together with the vegetation surrounding them at the height of 2.5 cm in mid July to simulate the traditional treatment of the grasslands.

Results

Seasonal development of the F. rubra stands

The overall pattern in the *F. rubra* population was fairly similar among years. Before the clipping (in late spring and early summer) the lengths of leaves of sterile tillers increased more than twofold; it sharply decreased owing to clipping, increased slightly again in late summer and decreased in autumn. Mean number of leaves of sterile tillers decreased slightly before clipping, increased after the clipping and remained stable or decreased in autumn (Fig. 1).

Natality was highest in spring; it decreased sharply before the clipping and remained low for the rest of the vegetation period. There was no flush of tiller formation in late summer after the clipping. Mortality was rather variable, but showed much less regularity than natality. It generally exceeded natality in summer and autumn (Fig. 2, Fig. 3). In some years (1988, 1990), there was a marked increase in tiller mortality in summer; in 1990 it was due to the abundant flowering. Total number of tillers increased every spring owing to the increase in natality, and slightly decreased in autumn and in winter (Fig. 3). Since natality exceeded mortality over a substantial part of the observation period, the net number of living tillers increased (Fig. 3).

Life span and survival of tillers

Out of the total population of 1251, life span is known for 636 tillers; 27 tillers were alive during the whole observation period and hence their life span exceeded 1128 days (3 and half years). Life span of 588 tillers is unknown.

In general, tillers survived for a rather long time. Out of the 1987 (i.e. those born in 1987) cohort, 14.5% tillers (30 out of 209) were still alive at the end of the observation. Out of the tillers present at the beginning of the observation, 12.9% were alive at the end of the observation period. Mean survival time of tillers is 529.6 days (s.e. = 11.7, estimated using the Kaplan-Meier method). The age specific mortality in the 1987 cohort is more or less constant during the observation period (Table 1), indicating exponential survivorship (Deevey type II, McNaughton et Wolf 1979).

The majority of newly formed tillers are formed intravaginally (866 out of 1041, i.e.

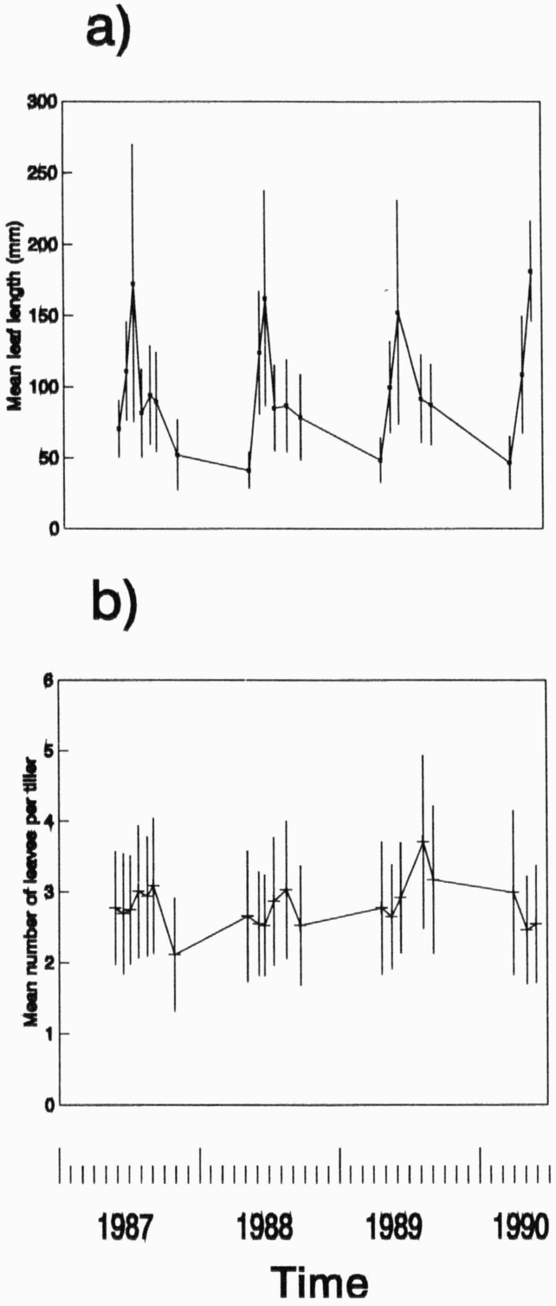

Fig. 1. - Seasonal change of the tiller size parameters: (a) mean length of the longest leaf and (b) mean number of leaves. Bars indicate ± 1 standard deviation.

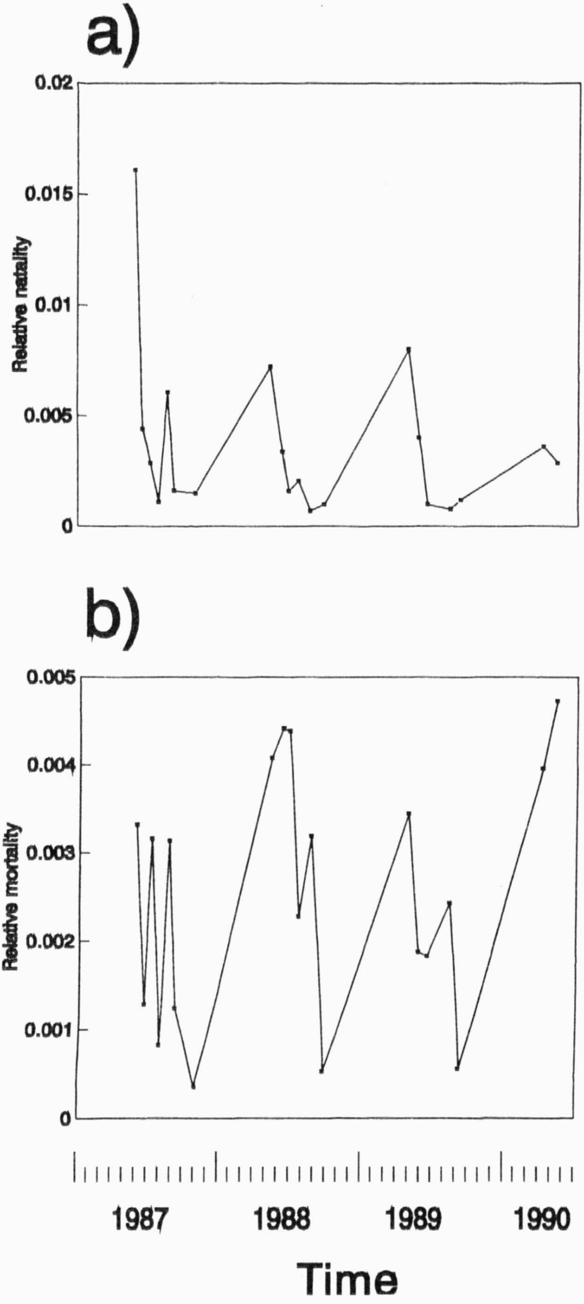

Fig. 2. - Time course of principal demography parameters: (a) relative natality and (b) mortality of tillers. Both variables are expressed per tiller and elapsed time since the preceding recording.

83 %), i.e. their mother tillers are known. By definition (see Methods section) mother tillers are not known for the extravaginal tillers. Therefore the statistics of daughter tiller production can be constructed for production of intravaginal tillers only. The average number of intravaginal daughter tillers produced per tiller is 0.586 annually. However, majority of tillers never form any intravaginal daughter tiller during their life. This is to a great extent due to differences in life span of potential mother tillers. The number of daughter tillers per tiller is strongly correlated with the life span of the mother tiller (Spearman's R=0.48, p<0.0001; see also Fig. 5).

In summer periods, smaller tillers seem to have larger probability to die than larger tillers (Table 2); in other seasons this difference was not significant.

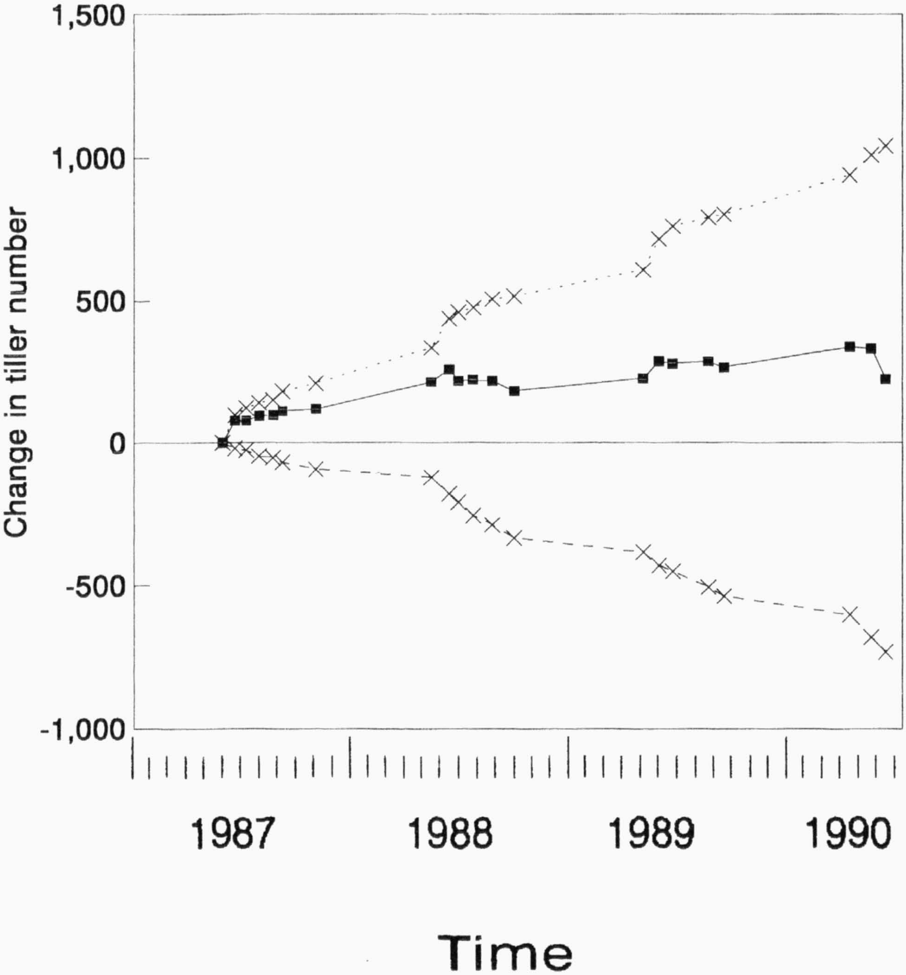

Fig. 3. - Number of living tillers (full line), cumulative births (dotted line) and cumulative deaths (dashed line) in the whole *Festuca rubra* tiller population.

Table 1. - Survivorship of tillers from the 1987 cohort.

Year %	surviving
<1 vegetation period	39.7
1-2 vegetation period	23.9
2-3 vegetation period	15.8
3-4 vegetation period	6.2
4 vegetation period	14.4

Table 2. - Difference in size between tillers which survived over at least two following recording periods and those which died in the immediately following period. The difference was tested using two tailed unpaired Student's t-test.

Recording period	Size measure	
	Leaf length	Leaf number
July 1987	<0.001	<0.05
November 1987	n.s.	n.s.
May 1988	n.s.	n.s.
July 1988	<0.001	<0.001
October 1988	n.s.	n.s.
May 1989	n.s.	n.s.
July 1989	<0.0001	<0.01
October 1989	n.s.	n.s.

Table 3. - Proportion of flowering tillers in the whole tiller population over the observation period.

Year	1987	1988	1989	1990
Total number of flowering culms	17	34	32	89
Proportion of total living tillers	5.9%	8.0%	6.6%	20.6%
Proportion of mortality at the clipping time	81%	66%	58%	
Proportion of mortality of the whole year	14%	13%	15%	

Flowering

F. rubra flowers in early summer; no flowering after the clipping was observed. The flowering resulted invariably in the tiller death. The proportion of flowering tillers varied significantly among years (from 5.9% to 20.6%; chi-square=49.1, $P<0.0001$). The mortality due to flowering represented 13 to 15 % of the overall mortality of the year; however, it accounts for 58 to 81 % of the mortality occurring at the clipping time (Table 3).

Average life span of flowering tillers is significantly greater than of those which do not flower (and hence die in other way; 492 vs. 316 days, Mann-Whitney test Z=11.01, P<0.0001). However, the life span of tillers that flower is extremely variable (Fig. 4). Sometimes, the tillers formed in early spring flower the same year; in contrast, some flowering tillers are 3 and more years old.

Flowering is well predicted by the tiller size in the previous year (Table 4). The prediction is similar both for number of leaves and leaf length; statistically bigger size in flowering tillers is invariably apparent in autumn of the previous year, though in some years it occurs also in summer and even spring of the previous year.

The number of daughter tillers differs between tillers that flower and those which die in another way (Fig. 5). The number of daughter tillers per tiller is not a Poisson distributed variable (Fig. 5).

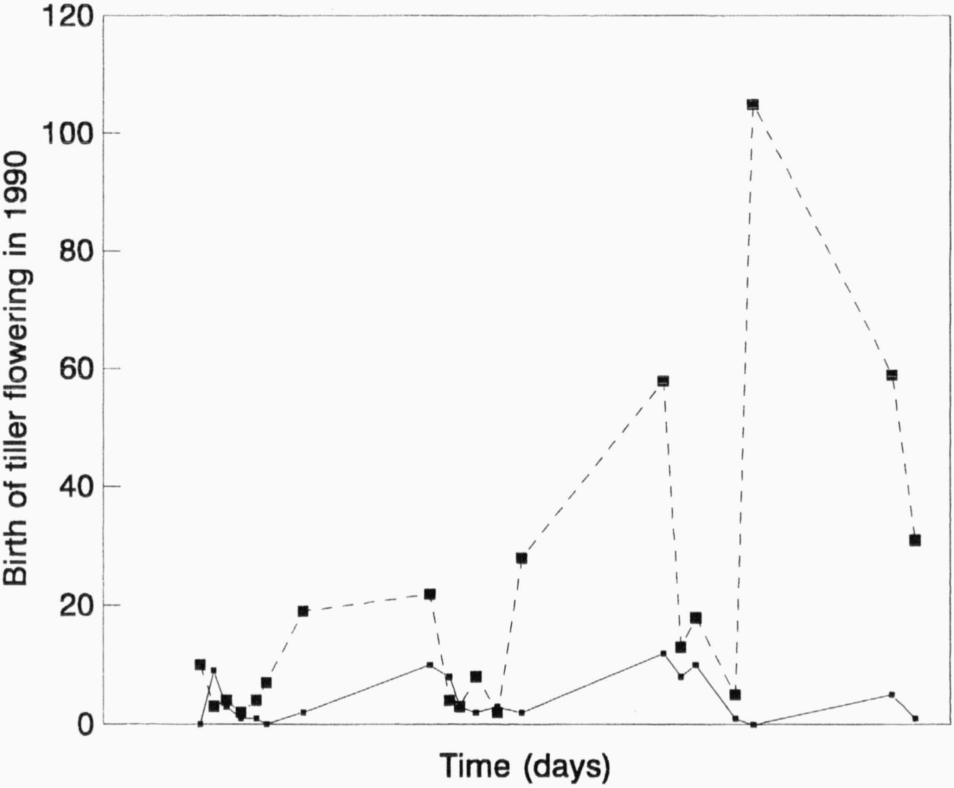

Fig. 4. - Distribution of births of tillers alive in summer 1990. Full line - tillers flowering in 1990, broken line - tillers not flowering in 1990. Both curves are significantly different using Kolmogorov-Smirnov two sample test (DN=0.529, P<0.05).

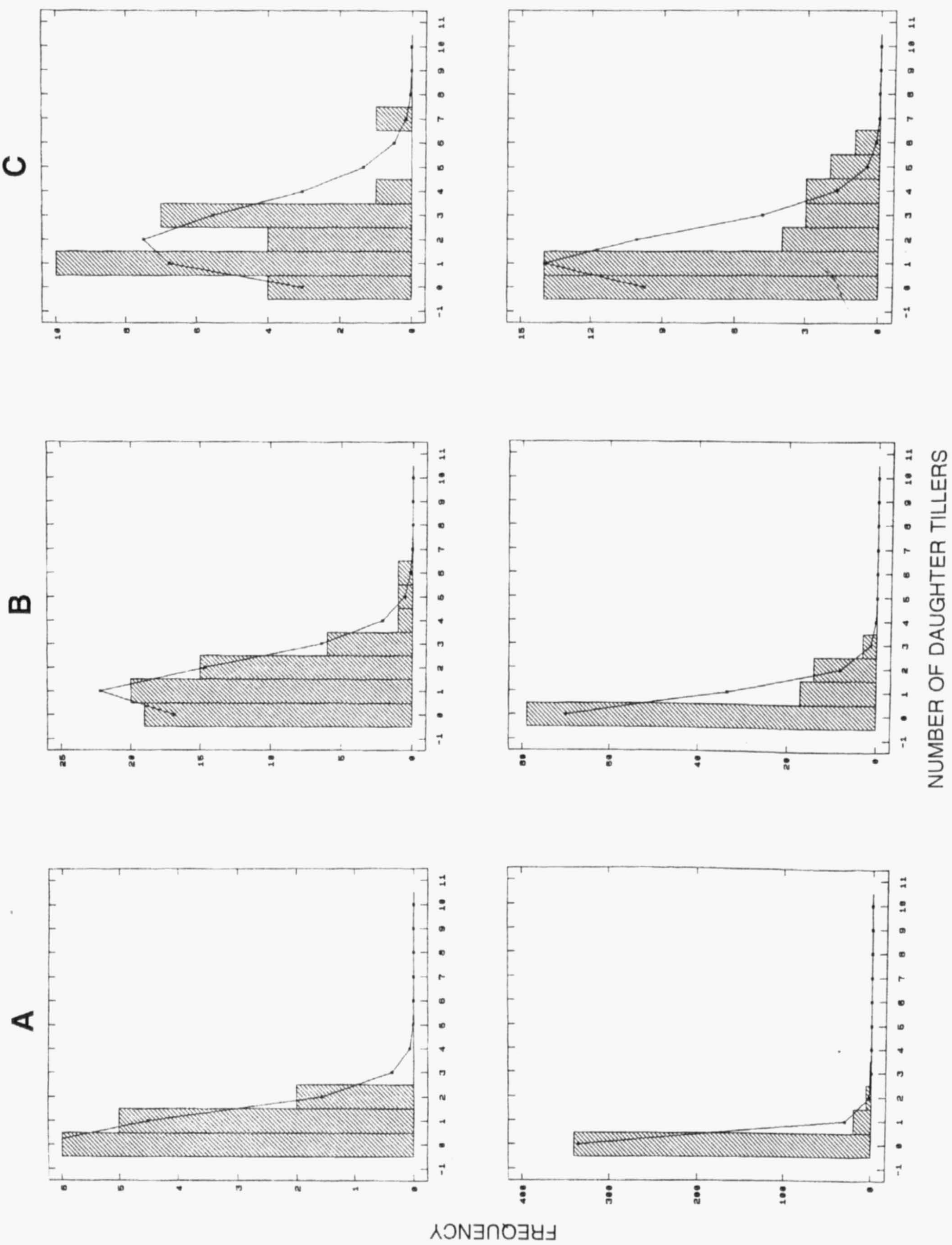

Fig. 5. - Relation between the life span, flowering and the distribution of the number of daughter tillers produced over the whole life of the tiller. Upper row - flowering tillers, lower row - not flowering tillers (i.e. dying from other causes). A - life span less than 365 days, B - life span 365-730 days, C - life span 730-1095 days.

Table 4. - Difference in size between tillers that flower in the following year and those remaining sterile in the following year.

Date of comparison	Size measure Leaf length	 Leaf number
Flowering in 1988		
November 1987	0.00527	0.00058
August 1987	<0.0001	0.024
July 1987	n.s.	n.s.
June 1987	n.s.	n.s.
Flowering in 1989		
October 1988	0.0003	0.0018
July 1988	0.0088	n.s.
May 1988	0.021	n.s.
September 1987	n.s.	n.s.
Flowering in 1990		
October 1989	<0.0001	0.015
July 1989	<0.0001	<0.0001
May 1989	0.00037	0.012
September 1988	n.s.	0.042
July 1988	0.026	n.s.
May 1988	n.s.	n.s.

Discussion

In clonal plants, demography of modules is intimately linked to morphogenetic processes of module formation. Two processes are involved here: (i) the potential number of newly born tillers is limited by number of buds, which is equal to the number of leaves, and (ii) physiological connections between tillers may play a role in determining their fate. The number of buds is clearly not limiting for tiller natality in the studied grassland, since the ratio of daughter tillers to leaves is on the average 1:3.5-4.5 (Hájek 1989). In contrast, mother/daughter tiller relationships play an important role. Since it ignores the clonal structure of the stand, a simple demographic approach adopted here cannot take these relationships into account. However, it still can describe at a phenomenological level many processes important for the sward.

The overall time course of the *F. rubra* tussock development in the mountain grassland does not differ from other grassland systems. Quite obviously, the lengths of leaves follow the course of mowing (or clipping), increasing sharply before the clipping. Owing to harsh mountain conditions, there was almost no average leaf length increase after the clipping. Number of leaves shows a reverse trend, decreasing before the clipping and increasing after the clipping. Both clearly respond to shading by taller and denser canopy in summer and to opening of the canopy after the mowing.

The spring flush of intravaginal tiller formation and the subsequent decrease of tillering in the flowering period is a well known phenomenon (Rabotnov 1985, Colvill et Marshall 1984, Butler et Briske 1988), though the published data on *F. rubra* (Serebrjakova 1968) report weak tillering in spring. In many grassland systems (Colvill et Marshall 1984 and references therein) there is also a characteristic increase in tiller formation in late summer. This was also described from *F. rubra* by Serebrjakova (1968) from the Moscow region. The absence of the late summer tillering of *F. rubra* in the present study is most probably due to high mountain conditions. Clones of *F. rubra* collected at the same locality and cultivated in lowlands did show a strong increase in tiller formation in late summer, whereas the same clones cultivated in mountain conditions did not (Hájek 1989).

Whereas the time course of natality is clearly unimodal and follows the vegetation development in the grassland, the mortality changes much less regularly during the year, indicating that there are several independent processes involved. Flowering accounts only for a minor part of observed deaths; this is in agreement with other reports from grasses in natural habitats (Mitchley 1988, Jónsdóttir 1991). The cause of the remaining deaths is uncertain and cannot be established using the present data set. The reduction in size of tillers before their disappearance is observable only in the summer period. This size decrease could be due either to (i) a positive feedback speeding up the tiller death in the period of intense competition for light, or (ii) active „shedding" of weak tillers by growing plants (Ong et Marshall 1979). The difference between summer period (with higher competition for light due to tall vegetation) and the rest of the year is striking. This does not mean there is not a similar decrease in physiological size in other periods; it only need not be measurable by the employed size variables (cf. de Kroon et al. 1992).

Quite surprisingly, flowering of tillers is rather unpredictable process. It is not related to the tiller age; tillers flowering in a particular period may differ in their age by a factor of four. The flowering induction in perennial grasses is a rather complicated and not well understood process; the differences between species are tremendous (Latting 1972, Sachs 1972). Experimental observations in *F. rubra* show that tillers are able to receive induction signals for flowering rather soon after their birth (Meijer 1984). In contrast, size of the tiller in a previous season is an important predictor of the incidence of flowering, though the patterns of prediction differ very much from year to year. The prediction by size is only statistical; there is no minimum size limit required for flowering, just as there is no maximum size which would guarantee flowering. The tiller size probably acts only by increasing the sensitivity to the induction signal.

The reasons for the overall increase in the tiller number over the observation period is not fully certain. A major cause may be some internal cyclicity of the tussock development as described e.g. by Uranov and Smirnova (Uranov et Smirnova 1969, Rabotnov 1985). The way how tussocks were selected (see the Methods section) could play a role in nonrandom distribution of stages of the internal tussock developmental cycle. Possibly some external cyclicity (e.g. climatic) longer than the observation period may also be involved. The strong proportion of flowering tillers in 1990 in all tussocks probably indicates presence of an external forcing. The observation period might be too short to study such cycles.

One of the striking features of the *F. rubra* demography in the mountain grassland is the large year-to-year variability in many parameters. This involves large variation in proportion of flowering tillers between years, in predictors of flowering between years, different tiller mortality between years etc. The similar variation is found also between tussocks (in life span, proportion of extravaginal tillers etc., cf. Krahulec et al., unpubl. data) and between behaviour of *F. rubra* in different regions (Serebrjakova 1968). This seems to be a more general feature of managed grassland systems, both at the level of between-species interactions (Herben et al. 1990, Herben et al. 1993b) and of individual species. It may be a component of the capacity of these grasslands to buffer varying environmental driving forces (Chesson et Huntly 1989).

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Souhrn

Článek přináší základní údaje o demografii odnoží u *Festuca rubra* v druhově chudé horské louce. Natalita odnoží byla nejvyšší na jaře; nepozorovali jsme v literatuře popisovaný nárůst natality po posekání louky. Naproti tomu mortalita odnoží byla rozložena více méně rovnoměrně během vegetační sezóny; to ukazuje na přítomnost několika vzájemně nezávislých příčin mortality. Kvetení mělo za následek odumření odnože; vcelku však pouze 13-15 % celkové mortality odnoží padá na vrub kvetení. Kvetoucí odnože jsou větší než nekvetoucí již v sezóně, která předchází kvetení, ale intenzita tohoto rozdílu se velmi liší mezi jednotlivými sezónami. Délka života odnoží je velmi variabilní, od několika týdnů až po několik let. Z odnoží, které byly přítomny na počátku pozorování, bylo přítomno ještě 12.9 % i na konci po třech a půl roce. Přežívání odnoží je zhruba exponenciální.

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