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TILLER DEMOGRAPHY OF *FESTUCA PALLENS* HOST (GRAMINEAE) IN TWO DRY GRASSLAND COMMUNITIES

ABSTRACT: Tiller demography of a perennial caespitose grass *Festuca pallens* Host was studied on permanent plots in two types of dry grasslands. The field work was done in the Považský Inovec Mts. (Western Carpathians) during 1993–1995. The permanent plot in the *Poo badensis-Festucetum pallentis* was located on a steep, strongly eroded S-facing slope covered with dolomit outcrops, scree and sparse vegetation (20%) dominated by *Festuca pallens*. The permanent plot in the *Festuco pallentis-Caricetum humilis* was located on the even ridge plateau with shallow stony soil and vegetation covering about 70% dominated by *Carex humilis* and *Festuca pallens*. The aim was to estimate the basic characteristics of tiller life cycle in *Festuca pallens*: tillering, flowering, mortality and life span. Tillers of *Festuca pallens* are exclusively intravaginal with a leaf rosette and polycyclic (can live for more than three years). A proximate maximum life span of orthotropic tiller parts was five or six years. The proportion of flowering tillers in the studied populations varied between the years from 3% to 10%. The mortality of tillers due to flowering represented about 50% of the overall tiller mortality. Flowering was mostly accompanied by an intensive pregenerative tillering. Tillering culminated twice a year – in spring and in autumn. About a quarter of the axillary buds developed into daughter tillers immediately after their formation. The fate of tillers in terms of survival, flowering and daughter tiller production can be predicted by their size. Both components of tiller size – leaf number and leaf length – influenced the fate of tillers although the predictive ability was stronger for leaf number. The two studied populations differed significantly in leaf number, leaf length and the height of inflorescences. These characteristics are supposed to be determined by external habitat conditions. The individual tiller life cycle (survival, life span, daughter tiller production) did not differ between the populations, thus the factors by which it is determined seem to be identical. These results support the idea that the basic processes and structures of tiller ontogeny are internally fixed for each species while external environmental conditions can only induce variability in absolute size.

KEY WORDS: caespitose grasses, tillering, flowering, life span, size-dependent tiller fate, dry grasslands

1. INTRODUCTION

Perennial caespitose grasses are clonally growing plants (Wilhalm 1995, Briske and Derner 1998). The clonal growth i.e. the lateral spreading through the iterative addition of modules is performed by tillering. Tillers represent one of the structural units of grasses and the knowledge of their life cycle and dynamics is important for understanding the life cycle and dynamics of whole tussocks (Serebrjakova 1971, Smirnova *et al.* 1976, Gatsuk *et al.* 1980).

As in all grasses, the fundamental growth unit is the metamer which consists of a blade, sheats, node, internode, axillary bud and perhaps adventious roots. A tiller develops from a bud in an axil of a leaf. The leaves of tillers also subtend axillary buds which in their turn may form further tillers, and this process – called tillering – can be repeated many times thus giving rise to a hierarchy of shoots.

In general, the intravaginal tiller grows parallel with the axis of its mother tiller covered by the sheath of the lower leaf and later it deviates in a certain angle. Following its appearance a tiller normally produces its own adventitious root system, although it remains in vascular connection with its mother tiller. The question of whether tillers function as independent units or if they are physiologically interdependent has frequently been discussed (e.g. Pitelka and Ashmun 1985, Wilhalm 1995).

The sole process of tillering was studied mostly in economically important grasses such as cereals and fodder grasses (for review see e.g. Langer 1963, Holmes 1989). Most of these results were obtained in experimental conditions. Recently, much attention has been paid to evaluate processes and mechanisms influencing tiller demography within individual clones and to assess mechanisms conferring ecological success to caespitose grasses (Briske and Derner 1998). Physiological integration of tillers within tussocks and its effect upon resource allocation has been studied (e.g. Wilhalm 1995, Alpert and Stuefer 1997). To understand all these complex processes and mechanisms, data are necessary of as many species as possible in various types of habitats. Studies of plant behaviour in natural conditions are inevitable.

This paper is devoted to tiller demography of *Festuca pallens* – perennial caespitose grass with xeromorph structure. Data were recorded on permanent plots in the natural environment of the studied species. Two types of dry grasslands were used as the background of the study as they represent two contrasting environmental conditions. Tiller demography aspects were compared and discussed in these contrasting systems to evaluate the possible effect of stress (xericity) upon the species traits at the structural level of tillers. The main goals of this paper are:

– to characterise the life cycle of tillers in *Festuca pallens*,

– to estimate the demographic features of tillers such as natality, mortality, life span, daughter tiller production and flowering,

– to estimate the variability of demographic characteristics by comparing populations in two different plant communities,

– to investigate the fate of individual tillers (in terms of survival, flowering and clonal growth) in relation to their size in the previous growing season.

2. MATERIALS AND METHODS

Festuca pallens Host is a polycarpic perennial caespitose grass. It produces intravaginal tillers with a leaf rosette (according to the classification of Serebrjakova 1971). It has submediteran-subatlantic distribution in Europe (Hegi 1998). In the West Carpathians *Festuca pallens* inhabits steep rocks or slopes with shallow rocky neutral to alkaline soils exposed to solar radiation exposed. It is the characteristic species of the *Seslerio-Festucion pallentis* (Hegi 1998) where it belongs to the earliest colonisers and dominants.

The field work was done in the Považský Inovec Mts. (Western Carpathians, 48°39′25″N, 17°54′20″E) in the top parts of a ridge running in the east-west direction at an altitude of 380-390 m. At the location, the Triassic dolomite supports shallow protorendzina soils. The whole area has a warm climate with mean annual temperature 9.2°C and the mean annual precipitation 625 mm at the nearby located climatic station Piešťany.

Phytosociologically, the studied communities belong to the class *Festuco-Brometea* Br-Bl. et R.Tx. 1943 and the associations *Festuco pallentis-Caricetum humilis* Sillinger 1930 corr. Gutermann et Mucina 1993 and *Poo badensis-Festucetum pallentis* Klika 1931 corr. Zolyomi 1966 (Mucina and Kolbek 1993). In the further text the abbreviated names *Poo-Festucetum* and *Festuco-Caricetum* will be used. The studied grassland sites have not been managed for at least 25 years.

The permanent plot in the *Poo-Festuce-*

tum was located on a steep strongly eroded south-facing slope covered mostly by dolomit outcrops and scree (Table 1). Due to the slope and low biomass production the soil cover is not developed. Vegetation cover is about 20% dominated by *Festuca pallens*. Other relatively abundant species are *Thymus praecox* Opiz, *Draba lasiocarpa* Rochel, *Teucrium montanum* L. and *Alyssum montanum* L. The cover of cryptogams varies significantly during the year reaching their maximum in autumn. The permanent plot in the *Festuco-Caricetum* was located on the ridge plateau with even surface only slightly inclined towards the ESE (Table 1). Soil is shalow and stony but builds more or less continuous layer. Vegetation covers about 70%. *Festuca pallens* and *Carex humilis* Leyss. dominate the stand and determine the overall vegetation structure. The gaps in the vegetation are frequently inhabited by lichens and mosses. Among the vascular plants the following belong to the more abundant: *Fumana procumbens* (Dunal) Gren. et Godr., *Teucrium montanum, Potentilla arenaria* Borkh., *Globularia punctata* Lapeyr., *Helianthemum grandiflorum subsp. obscurum* (Pers. ex Wahlenb.) Holub and *Sanguisorba minor* Scop.

In each type of dry grassland a permanent plot of 2 m^2 was established. In May 1993 two hundred vegetative tillers were chosen at random within each permanent plot. Plastic marks differing in colour and number were placed on each tiller below the lowest leaf blade. All the younger leaves and daughter tillers produced later appeared within the markings of the mother tiller. No adverse effect of such marking upon tiller performance was recorded, although no experiment was done to confirm it.

Leaf and tiller characteristics were recorded in three week intervals during the growing season 1993. Number of living and dead leaves and their position on the tiller were recorded at each census. Leaves were considered to be alive if they contained at least some green parts and dead if they were either completely dry or yellowing without green parts. Leaf blade length of three leaf cohorts was measured to the nearest millimetre. Final length of a leaf blade after its growth has ceased was used for analyses. In 1993, thirty generative tillers were chosen at random in each population to measure the height of inflorescence and the number of spikelets in panicles.

Tiller observations continued until October 1995, tiller fate was recorded at the following dates: May 1993, September 1993, May 1994, October 1994, May 1995 (only *Poo-Festucetum*), October 1995. Newly established, dead and flowering tillers were recorded. Using these data, tiller survival was analysed by a

Table 1. Characteristics of permanent plots where tiller demography of *Festuca pallens* was studied. Permanent plots are designated according to the vegetation type.

	Poo-Festucetum	*Festuco-Caricetum*
Altitude (m)	380	382
Aspect (degrees)	180	105
Slope (degrees, average of 8 measurements)	28	6
Soil depth (cm, average and range of 80 measurements)	4.8 (1.8–7.2)	4.8 (4.3–5.9)
Potential direct solar irradiation (kJ m^{-2} s^{-1}, average of 8 measurements)	76.5	66.5
Soil pH	7.4	7.0
Humus content (%)	5.3	13.4
Content of soil particles <0.002 mm (%)	2.1	6.6
Content of soil particles 0.002–0.1 mm (%)	39.6	67.1
Content of soil particles >0.1 mm (%)	58.3	26.3
Vegetation cover (herb and moss layer, %, average of 8 estimates)	20	70

linear regression and the life span of tillers was estimated. Tiller half-life is the time in which 50% of tiller sample will die. All data concerning the life span of tillers are related to the life cycle of the orthotropic assimilating part of tillers. The life of axillary buds and plagiotropic parts of tillers were not studied.

Because in the *Festuco-Caricetum* tiller fate was not recorded in spring 1995, most presented results come only from one transition period (1993–1994). Fate of tillers up to May 1994 was analysed in relation to their size in 1993. Two non-destructive measures of tiller size were estimated: the number of leaves produced within the growing season (in the text abbreviated as *leaf number*) and the length of the longest leaf blade (*leaf length*, not necessary the leaf which extends to the highest point of tiller). They can easily be determined and their predictive value for tiller biomass is assumed to be high (Herben *et al.* 1993a). The correlation between *leaf number* and *leaf length* was poor (r = –0.15 for the *Poo-Festucetum* and r = –0.05 for the *Festuco-Caricetum*). They represent different components of tiller size. *Leaf number* represents the number of structural units of the tiller (metamers), while the *leaf length* represents the size of individual metamers. Furthermore, tiller size in five time periods during the growing season was determined by the number of living assimilating leaves. Opposite to *leaf number* it is a static variable reflecting an immediate state of the tiller and it was also analysed in relation to the tiller fate.

The daughter tiller production during 1993–1994 was related to the size and developmental stage of individual tussocks. Two size categories of tussocks were distinguished: small tussocks up to 15 tillers and big tussocks with 15 and more tillers. Daughter tiller production was studied separately in vegetative and generative tussocks as well as in progressive (growing in size during 1993–1995) and retreating tussocks (stable or declining in size during 1993–1995). As no clonal fragmentation with subsequent rejuvenation was observed it is assumed that in most cases the recorded tussocks were equivalent to genets. However, no attempt to verify this was done and therefore several tussocks might have belonged to the same genet.

3. RESULTS

3.1 Tillering

During May 1993 – May 1994 most of the survived tillers have produced daughter tillers (78% in the *Poo-Festucetum* and 75% in the *Festuco-Caricetum*). There was no significant difference between the populations in daughter tiller production of surviving tillers (χ^2 test, $\chi^2 = 2.25$, $P = 0.522$).

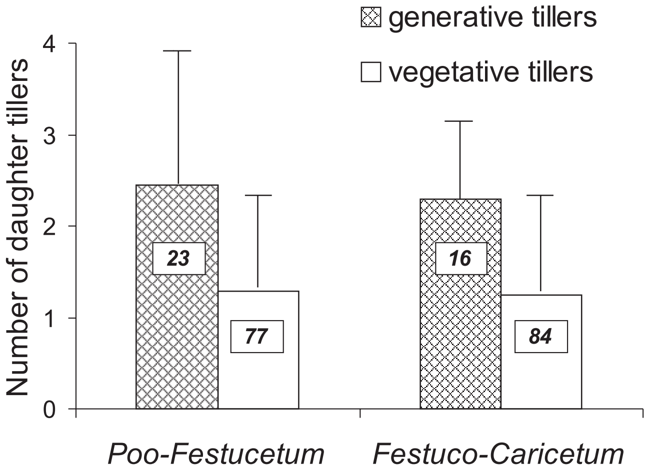

Fig. 1. Average number of daughter tillers of *Festuca pallens* produced from May 1993 until May 1994 by generative and vegetative tillers in the two studied populations. Standard deviations are depicted by lines and proportion (in %) of individual tiller groups in the studied population is shown in the middle of each bar.

Two main periods of daughter tiller formation were recorded – autumn and spring. Usually, two to three daughter tillers per year arised in the axils of succeeding leaves that were formed during summer and autumn. The axillary bud belonging to a given metamer did not develop into a new daughter tiller until the leaf of the older metamer has ceased expansion. The first daughter tillers appeared out of a covering sheaths at a time when a covering leaf blade started to die at its top. Some tillers have not produced daughter tillers during their whole life. In the studied populations tillers were observed without any sign of tillering during three growing seasons. They represented 3% of tillers in the *Poo-Festucetum* and 12% in the *Festuco-Caricetum*. About a half of them continued their life after the observation period has ceased.

Theoretically, the number of leaves on a tiller determines the number of axillary buds from which daughter tillers can develop. About a quarter of the axillary buds developed into daughter tillers immediately after their formation (buds established during 1993 and daughter tillers developed until May 1994 were involved in the calculation). The average proportion of developed daughter tillers was 26% in the *Poo-Festucetum* (n=127) and 27% in the *Festuco-Caricetum* (n = 135). The difference between the two populations was not significant (Mann-Whitney test, *P* = 0.511). The ratio of daughter tillers to axillary buds was 1:3.2 to 1:5.2 in the *Poo-Festucetum* and 1:2.9 to 1:4.9 in the *Festuco-Caricetum*.

Flowering was mostly accompanied by an intensive pregenerative tillering. Significant difference in daughter tiller production was found between flowering and vegetative tillers (Fig. 1). In both populations tillers that flowered in 1994 produced significantly more daughter tillers during the previous year than the vegetative tillers (Mann-Whitney test, P=0.000 for both *Poo-Festucetum* and *Festuco-Caricetum*).

The correlation between tussock size (expressed as number of tillers in tussock) and number of daughter tillers produced by surviving tillers was not found in any population (Spearman rank correlation coefficient R = 0.066, *P* = 0.451 in the *Poo-Festucetum* population and R = 0.031, *P* = 0.709 in the *Festuco-Caricetum* population). In both populations, small and large tussocks did not differ in number of daughter tillers produced per surviving tiller from May 1993 until May 1994 (Table 2). In the *Festuco-Caricetum* the average number of daughter tillers per surviving tiller was significantly higher in generative tussocks than in vegetative ones. In the *Poo-Festucetum* the difference was at the border of statistcal significance (Table 2). Tillers producing no daughter tillers were present in all stages of tussock development. Their proportion was similar in small (39% and 32%) and big tussocks (25% and 37%) as well as in vegetative (39% and 43%) and generative tussocks (35% and 67%, first value always for the *Poo-Festucetum* and the second one for the *Festuco-Caricetum*).

Table 2. Tillering of *Festuca pallens* in relation to tussock development. Average number ± standard deviation of daughter tillers produced per surviving tiller from May 1993 until May 1994 are shown for tussocks of different size (small: 1–14 tillers, big: ≥ 15 tillers) and stage. *P*-values of Mann-Whitney test are given for differences between tussock categories within each of the studied population. The proportion (in %) of tussock categories in the total number of tussocks studied is given in parentheses.

Tussock category	*Poo-Festucetum*		*Festuco-Caricetum*	
small	1.50±1.29	(81)	1.52±1.23	(50)
big	1.56±1.00	(19)	1.39±1.03	(50)
	P=0.512		*P*=0.692	
vegetative	1.32±1.20	(46)	1.16±1.03	(40)
generative	1.70±1.26	(54)	1.65±1.16	(60)
	P=0.081		*P*=0.019	

3.2 Mortality and life span of tillers

The only dramatic changes in tiller survival from May 1993 until October 1995 were recorded after the death of flowering tillers during June-July (Table 3). The mortality of tillers due to flowering represented about 50% of the overall tiller mortality. Tiller mortality by other reasons than flowering did not culminate within a certain period of the year but was rather uniformly distributed between seasons. In the population of *Poo-Festucetum* the size of tussocks was significantly higher for tillers that died than for tillers that survived (Mann-Whitney test, P=0.000). In the *Festuco-Caricetum* population no differences in tussock size between dead and surviving tillers were found (Mann-Whitney test, $P = 0.432$).

Similar trends can be found to govern tiller survival in both populations. As the study period was too short for a precise estimation of tiller half-life, it can be assessed only approximately. There are only minor differences in course of survival between the studied populations (Table 3). As vegetative tillers were chosen at random their age at the beginning of the observation could differ significantly (it was not a cohort of tillers). Thus the maximum life span of *Festuca pallens* tillers can be five or six years. Most tillers are supposed to live for two to four years.

3.3 Flowering

Tillers either completed their life cycle by flowering or remained vegetative. The proportion of flowering tillers in total tiller number within the permanent plot varied between the years from 3% to 10% (in 1993 it was 3.4% and 6.3%, in 1994 it was 8.8 and 9.1 in the *Poo-Festucetum* and the *Festuco-*

Table 3. Tiller survival of *Festuca pallens* from May 1993 until October 1995 in the studied populations, veg – vegetative tillers, gen – generative tillers.

Poo-Festucetum			
Date of recording	Number and type of tillers that died since the last recording	Surviving tillers (%) since the last recording	Surviving tillers (%) since the beginning of observation
1993 May	0	100	100
1993 Sept	16 of 172 (veg)	91	91
1994 May	19 of 156 (veg)	88	80
1994 July	31 of 137 (gen)	77	62
1994 Oct	6 of 114 (veg)	95	58
1995 Oct	21 of 116 (veg+gen)	82	48

Festuco-Caricetum			
Date of recording	Number and type of tillers that died since the last recording	Surviving tillers (%) since the last recording	Surviving tillers (%)since the beginning of observation
1993 May	0	100	100
1993 Sept	17 of 178 (veg)	90	91
1994 May	16 of 161 (veg)	90	82
1994 July	23 of 145 (gen)	84	69
1994 Oct	12 of 141 (veg)	92	63
1995 Oct	29 of 122 (veg+gen)	76	48

Caricetum, respectively). Flowering started in April and continued until June. After seed ripening in July the orthotropic part of the tiller died. All flowering tillers (except one in the *Poo-Festucetum*) produced daughter tillers.

The average height of inflorescence was 23.7 cm in the *Poo-Festucetum* population and 27.8 cm in the *Festuco-Caricetum* population (t-test, *P* = 0.001). The culm was formed by two or three longer internodes and one or two nodes with short leaves (1–2 cm). There were no differences in the number of spikelets in panicles between the populations (t-test, *P* = 0.212), the average values were 13 in the *Poo-Festucetum* and 14 in the *Festuco-Caricetum.*

3.4. Tiller size

The average number of leaves produced by a tiller from May 1993 until May 1994 (*leaf number*) was 5 with a range of 1–10 leaves. The two studied populations differed significantly in *leaf number* (t-test, *P*=0.000). The mean number of leaves produced by surviving tillers was higher in the *Poo-Festucetum* (mean 5.81, SD=1.16) than in the *Festuco-Caricetum* (mean 5.28, SD = 0.84).

Number of living assimilating leaves in tillers increased progressively during the growing season 1993 and the variance of data increased simultaneously (Fig. 2). From May until end of July number of living leaves in the *Poo-Festucetum* was significantly higher (t-test, in all cases *P* <0.001) than in the *Festuco-Caricetum* population. In September no significant difference was found in number of living leaves between the populations. Number of dead leaves per tiller counted in May 1993 was significantly higher (t-test, *P* <0.000) in the *Poo-Festucetum* (mean 2.23, SD = 1.18) than in the *Festuco-Caricetum* (mean 1.3, SD=0.94).

The maximum length of leaf blade in tillers varied between 15 and 137 mm. Tillers in the *Festuco-Caricetum* had significantly higher *leaf length* (mean 6.81 cm, SD = 2.06) than tillers in the *Poo-Festucetum* (mean 5.63 cm, SD = 2.20, t test, *P* <0.000, only surviving tillers were included into the analysis).

3.5 Size-dependent tiller fate

Both *leaf number* and *leaf length* influenced the fate of tillers in the following growing season (Table 4). Larger tillers showed an increased incidence of both flowering and daughter tiller production and a decreased incidence of death in the subsequent time period. This predictive ability of tiller fate

Table 4. Tiller size components (*leaf number* and *leaf length*) of *Festuca pallens* in 1993 as predictors of tiller fate up to May 1994. Mean values ±standard deviation are shown with *P*-values of the t-test for differences in means of the compared groups (* – *P* <0.05, ** – *P* <0.01, *** – *P* <0.001, n.s. – not significant). Tiller survival was evaluated in vegetative tillers (flowering tillers were not included into analyses) and the daughter tillers production was evaluated in surviving tillers.

	Poo-Festucetum			*Festuco-Caricetum*		
Tiller survival (May 1994)						
	tillers died	tillers survived	*P*	tillers died	tillers survived	*P*
leaf number	4.22±1.14	5.81±1.16	***	3.64±1.08	5.28±0.84	***
leaf length	7.23±2.43	5.63±2.20	***	6.46±2.53	6.81±2.06	*n.s.*
Daughter tillers (DT) production (May 1994)						
	DT produced	DT not produced	*P*	DT produced	DT not produced	*P*
leaf number	6.02±1.10	5.13±1.02	***	5.40±0.87	4.94±0.63	**
leaf length	5.74±1.97	5.25±2.85	*n.s.*	6.87±2.11	6.62±1.91	*n.s.*
Flowering (May 1994)						
	generative tillers	vegetative tillers	*P*	generative	vegetative	*P*
leaf number	6.03±1.08	5.40±1.33	*	5.70±0.82	4.87±1.09	**
leaf length	6.67±2.25	5.94±2.39	*n.s.*	8.30±2.12	6.51±2.03	***

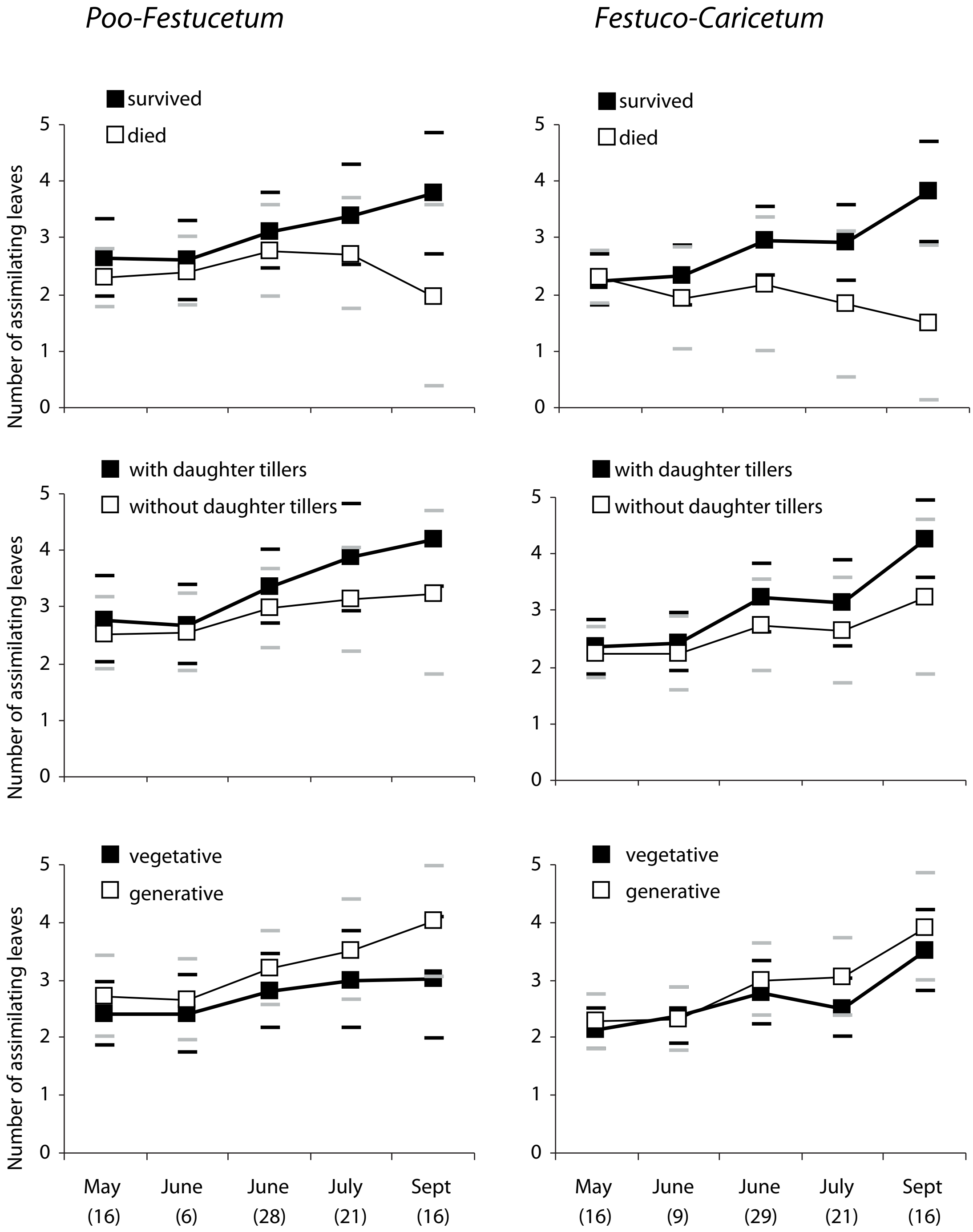

Fig. 2. Number of assimilating leaves in tillers of *Festuca pallens* as predictor of tiller fate in the populations of *Poo-Festucetum* (left) and *Festuco-Caricetum* (right). The variable was compared in relation to tiller survival (the upper row), daughter tiller production (the middle row) and flowering (the lower row). Differences between the compared groups of tillers were tested by the repeated-measures ANOVA, they were significant in all cases at $P < 0.001$.

was much stronger for tiller size expressed by *leaf number*. Its influence on tiller fate was significant in both populations for all studied characteristics. Moreover, *leaf number* was positively correlated with the number of daughter tillers produced in the subsequent period (r = 0.48 for the *Poo-Festucetum* and r = 0.50 for the *Festuco-Caricetum*). There was very poor correlation indicated between *leaf length* and the number of produced daughter tillers (r = –0.09 and r = 0.11 for populations in the *Poo-Festucetum* and the *Festuco-Caricetum*, respectively). Tillers with longer leaves showed no higher incidence of daughter tiller production than tillers with short leaves. Even the tiller survival was not affected by *leaf length* in the *Festuco-Caricetum* population. Suprisingly, in the *Poo-Festucetum* population tillers which died had significantly longer leaves than surviving tillers. The incidence of flowering was influenced by both components of tiller size – *leaf number* and *leaf length* and the prediction was about equally strong. Although there is a higher probability of flowering for larger tillers, there is not a minimum tiller size for flowering, just as there is no maximum size, which would guarantee flowering.

Tillers with various fate in relation to survival, tillering and flowering differed significantly in number of assimilating leaves (Fig. 2, according to the repeated-measures ANOVA all factors were significant: groups, time and their combination at $P < 0.01$). Number of dead leaves had no relation to tiller fate.

4. DISCUSSION

4.1 Tillering

There are numerous studies showing a seasonal pattern of tiller natality and mortality (see Noble *et al.* 1979 for references). A spring maximum in the production of intravaginal tillers was recorded for grasses in natural stands; grasses in cultivation were not influenced by changing seasons (Hájek 1989). The summer pause in most grass species is related to the correlative relations between the mother and daughter tillers (stalk prolongation and flowering), and to the lack of nutrients or light (Lebedev and Melnik 1959, Smelov 1966, Serebrjakova 1971, Colvill and Marshall 1984, Hájek 1989). In xerophilous steppe grasses such as *Festuca pallens* the summer pause in tillering is rather induced by a summer drought period. A winter interruption in tiller production is also generally observed and seems to be a result of reduced metabolism during severe weather conditions. During mild winters tiller development and growth may go on.

Not every metamer produces a viable bud and not every bud develops into a daughter tiller. In some nodes the axillary buds are not even established or they are not fully developed (Serebrjakova 1971). The development of daughter tillers from axillary buds depends on several factors. The correlative interrelations between tillers of various orders play an important role. Strong development of apical part of the mother tiller can damp tillering while the removal of apical meristems is followed by intensive tillering. Such apical dominance has been observed in a number of clonal plants (Jónsdóttir and Callaghan 1988). The distribution of mineral nutrients, hormonal regulation and external environmental conditions are also important. In our study daughter tillers were formed from about one quarter of all axillary buds. This number reflects only the period immediately following bud establishment, until the stage of active development of apical meristems in spring. The remaining buds may be unviable or they may develop into daughter tillers after a dormant period. Similar ratio of daughter tillers to axillary buds 1:3.5 to 1:4.5 was found in *Festuca rubra* (Hájek 1989). In other caespitose festucoid grasses such as *Festuca ovina* (Serebrjakova 1971), *Festuca sulcata*, *Koeleria gracilis* and several species of *Stipa* (Belostokov 1957) about one third of axillary buds develops into daughter tillers.

The comparison of daughter tiller production of vegetative and flowering tillers indicate that tiller production in *Festuca pallens* culminates before and during the development of inflorescence (prereproductive tillering). Long lasting and gradual prereproductive tillering occurs in many steppe grasses with polycyclic tillers (Serebrjakova 1971). Thus the idea of different predominant function of tillers with complete life cycle (seed production) and tillers with uncomplete life cycle (tillering to ensure vegetative reproduction) seems to be wrong.

Production of daughter tillers was not related to size of tussocks but was different for vegetative and generative tussocks as well as for progressive and retreating tussocks. It seems that the intensity of tillering can change during the tussock ontogeny culminating during both the virginile and early generative stages (in the later accompanied with the intensive pregenerative tillering).

4.2 Mortality and life span of tillers

The linear trend of survival was a good assumption and the line fits well although the sudden changes caused by the death of flowering tillers are present. This can be explained by the fact, that populations were composed of tillers of different age. If a tiller cohort would be observed, different trends of survival could be expected. In *Festuca rubra* young shoots had much higher probability of dying than older ones (Hara and Herben 1997). Once they have passed the first year of their life, their fate was independent of their age and was governed primarily by their size. On the other hand, survival of younger shoots exceeded the survival of older ones in *Carex bigelowii* (Carlsson and Callaghan 1990). Various experiences show that trends of survival may differ between species and also as a response to different environmental conditions.

The age-dependent mortality of tillers seems to differ from the age-dependent mortality of tussocks. In the latter, mature generative tussocks has the lowest mortality (e.g. Smirnova *et al.* 1976), while in juvenile and senescent individuals the incidence of dying is much higher. For tillers, flowering inevitably means the subsequent death. Thus some vegetative tillers with an uncomplete ontogeny can live longer than flowering ones (Belostokov 1957). On the other hand, Herben *et al.* (1993b) found that for *Festuca rubra* the average life span of flowering tillers was significantly greater than the one of tillers that did not flower, although the life span of tillers that flower was extremely variable.

The estimated maximum life span for tillers of *Festuca pallens* is 5 or 6 years. Of course not all tillers live that long, some complete their life cycle within one, two or three years. Also it can not be excluded that some tillers can live for more than six years. Anyway, tillers of *Festuca pallens* can be classified as polycyclic (Serebrjakov 1952). According to Serebrjakova (1971), tillers with a big leaf rosettes are often polycyclic (such tillers were recorded in *Festuca ovina* by Serebrjakova 1971, *Festuca varia* by Gogina 1961, *Deschampsia caespitosa* by Zhukova 1975, *Festuca sulcata* and *Stipa lessingiana* by Belostokov 1957). The reduction or prolongation of the life cycle can be influenced by environmental conditions (longer life span in nutrient poor conditions), the position of tiller within the individual tussocks and the general state of tussock (Belostokov 1957). On the other hand, maximum tiller life span of the North American species *Schizachyrium scoparium* and of most studied economically important loose-tussock grasses do not exceed two years (Langer 1956, 1972, Briske and Butler 1989, Welker and Briske 1992, Briske and Derner 1998).

All recent estimates of life span are related to the life cycle of the orthotropic part of tillers referred as the small life cycle. Besides that, the complete ontogeny of tillers comprises the stage of axillary bud development and the stage of secondary activity of plagiotropic parts (including the postgenerative tillering). The time of tiller persistence as a complex is known to be much longer (years or even decades) than the persistence time of its assimilating generative part (Serebrjakova 1971, Zhukova 1974, 1975, Callaghan 1976, Noble *et al.* 1979) and its life span seems to be species specific. Among the grass species the xerophytic caespitose grasses seem to have tillers with one of the longest life spans.

4.3 Flowering

Flowering in grasses is difficult to predict. It is not related to tiller age; tillers formed in early spring can flower the same year or many years later (Herben *et al.* 1993b). Most grass species of north temperate region are supposed to pass through winter conditions with low temperatures and/or short daylengths to flower (Holmes 1989) or the incidence of flowering is related to the development of some minimum number of leaves which is species specific (Serebrjakova 1971). Because the age of tillers in the studied populations was unknown at the beginning of the observations, the data can not be used for the estimation of age-dependency of flowering in *Festuca pallens*. Flowering of daughter tillers younger than one year was rare – three cases were observed (0.7% of young tillers, 5% of flowering tillers). All such tillers were formed during the late summer and flowered in the subsequent spring.

4.4 Tiller size

In *Festuca pallens* the total leaf production of tillers (*leaf number*) was higher in the *Poo-Festucetum*. So was the number of dead leaves per tiller and number of living leaves in summer measurements; the differences were not detected in autumn. An explanation can be an earlier phenological development in spring due to its location at the edge of south-facing slope and subsequently longer growing season.

Leaf length was bigger in the *Festuco-Caricetum* population. This can be a consequence of less extreme temperature- and water-regime in the habitat. The final length and form of leaves in grasses depends on temperature (Holmes 1989). Although leaves grow faster and larger at higher temperatures, their growth at extreme temperatures is restricted by drought. In *Festuca rupicola* and *F. valesiaca* leaf length changes proportionally to water supply (Hroudová-Pučelíková 1972). Another possible explanation is that the leaf length in *Festuca pallens* is influenced by the biotic environment. In denser stands of the *Festuco-Caricetum* leaves grow longer because of different red: far-red radiation ratio. Higher leaf production and higher number of living leaves in the *Poo-Festucetum* could also be an adaptation to hold a certain capacity for photosynthesis in conditions where the leaf length is restricted by drought and high temperatures (the shorter leaves in the *Poo-Festucetum* in summer).

4.5 Size-dependent tiller fate

The correlation between *leaf number* and number of daughter tillers produced in the subsequent period is probably a consequence of the fact that number of leaves is determined by the number of axillary buds from which daughter tillers may potentially develop.

In both clonal and non-clonal plants the shoot size may have a large effect on survival resulting in a relationship between size structure and shoot demography (Hara and Herben 1997). The predictive value of tiller size for tiller fate was shown by several authors (Carlsson and Callaghan 1990 for *Carex bigelowii*; Hara and Herben 1997 for *Festuca rubra*). Similar to our study, different components of tiller size differed in determining the fate of tillers. In *Festuca rubra* leaf length was the best predictor of daughter tiller production (Hara and Herben 1997). Moreover, the leaf length of mother tillers was strongly correlated with both leaf length and leaf number of daughter tillers. This relation was not found in *Festuca pallens* where leaf length had no predictive value for daughter tiller production.

When predicting tiller fate by their size, two aspects are important: a) which components of tiller size are measured and b) in which season these measurements are obtained. For *Festuca pallens* we found the following components of tiller size to be appropriate: 1) Number of leaves produced during a growing season. It includes the continuous growth activity of tiller and so well reflects the tiller's vitality processes. If only a single measurement of leaf number is possible, it should be done at the end of the growing season. 2) The length of the longest leaf blade preferably measured during a period following the maximum growth. The measurement of average leaf length is not appropriate as the individual metamers in tiller are not equivalent and the comparison of different leaf cohorts could be misleading. Based on our analyses and experience from literature (Hara and Herben 1997) it seems, that the most predictive results were based on measurements obtained during the period immediately preceding the studied process, e.g. if tiller death culminates at the end of the growing season, measurements should be done in summer; for spring flowering of tillers or tillering culminating in spring, autumnal measurements would be the most predictive. This is especially valid for prediction of flowering where the inflorescence initiation (or at least some related processes) may start as soon as during the late summer previous to flowering.

The size-dependent tiller fate of *Festuca pallens* has been studied only within one growing season. However, the life span of tillers in *F. pallens* is often much longer than one year. Therefore, if there are any between-year carry-over effects involving tiller size, year-to-year changes in size could have effects on population dynamics. Only long-term observations would resolve such a problem. However, Hara and Herben (1997) analysing data of such a long-term experiment found that tiller size variation in *Festuca rubra* was not related to the previous life history of individual tillers or their age. Tiller age was not a good predictor of tiller fate.

The idea of tiller differentiation can not be tested using our data although it is very probable that the basic tiller development is affected by tiller order and its location on mother tiller and within the whole tussock (as it was shown for some steppe xerophil grasses by Steshenko 1952 Belostokov 1957, Persikova 1959a,b, Serebrjakova 1971).

5. CONCLUSIONS

The growth, development and dynamics of modular organisms such as *Festuca pallens* inevitably depends on the life cycle and demography of its structural units – individual tillers. Tillers of *Festuca pallens* have several characteristics in common with tillers of other caespitose grasses, mostly those with a xeromorph structure inhabiting xeric habitats such as steppes or severe mountain grasslands.

Comparing the two studied populations at the structural level of tillers revealed differences in the following characteristics: leaf number, leaf length and the height of inflorescences. All these characteristics are quantitative and relevant for biomass production. They are thought to be determined by external habitat conditions. Still, the influence of genotypes can not be excluded as no genetical analysis was made. The tiller life cycle did not differ between the populations, thus the factors by which it is determined seem to be identical. The following characteristics were similar for both studied populations: mortality and life span of tillers, production of daughter tillers, proportion of axillary buds developed into the daughter tillers. These results support the idea that the basic processes and structures of tiller ontogeny are internally fixed for each species while external environmental conditions can only induce variability in absolute size.

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