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Leaf demography of *Festuca pallens* in dry grassland communities

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Abstract: Leaf blade parameters and leaf demography of *Festuca pallens* Host were studied in two types of dry grasslands. The field work was carried out 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 dolomite 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*.

In comparison to other grasses *Festuca pallens* had a very low rate of leaf turnover. The highest leaf birth rates and the lowest leaf death rates were observed in June. Leaf mortality was uniformly distributed in time without a distinct minimum or maximum. For the surviving tillers the leaf production exceeded the leaf mortality during the whole growing season. The steady net gain of leaves in tillers was not interrupted by the parallel process of tillering. Among the leaf cohorts the leaves produced in May had the longest leaf blades. Leaves grew during the whole year. The winter cold and summer drought might slow down the growth rate or interrupt the growth. The growth of a leaf blade took five to eight weeks. Leaf life span was estimated to 150–200 days (time from leaf appearance at the apex to the complete loss of its green assimilating parts). In comparison to other grasses *Festuca pallens* belongs to the species with the longest leaf life span. The effect of environmental factors on leaf demography was followed by the comparison of two populations belonging to two phytosociological associations differing mostly in habitat xericity. Differences were revealed in the following characteristics: length of leaf blade in cohorts born during May and June, maximum length of a leaf blade in a tiller and daily increments in May and June. The course of leaf natality and mortality was similar in the studied populations.

Key words: dry grasslands; leaf blade parameters; leaf turnover; leaf life span

Introduction

The understanding of dynamic aspects of plant organisms depends on awareness of the turnover rate of their parts. Leaf dynamics may be important for the understanding the dynamics of tillers or genets. Information on leaf life span is likely to be particularly relevant to e.g. nutrient cycling, herbivory or plant strategy (Chabot & Hicks 1982; Hendry & Grime 1993; Craine et al. 1999; Ryser & Urbas 2000).

The fundamental growth unit of grasses is the phytomer (metamer, module, phyton), which consists of a blade, sheath, node, internode, axillary bud and sometimes also adventitious roots (Serebrjakova 1971; Briske & Derner 1998). Tillers comprise a series of phytomers successively differentiated from individual apical meristems (White 1979). Morphological variation of individual ramets is a consequence of the number and size of the phytomers of which they are comprised.

A leaf (blade and sheath) is located at the top of the phytomer. Leaves are established from leaf primordia at the tiller apex. The prolongation of individual parts of phytomers follows the order: leaf blade, leaf sheath and internode. Growth is finished first in the apical parts of these organs (Serebrjakova 1971; Rytova 1967). The first leaf – prophyll – of the intravaginal tiller in *Festuca pallens* is simple and transparent with a protective function (personal observation). The following leaves are green with distinct blades and sheaths. In stable environments the length of succeeding leaves gradually increases following an unimodal curve, which is an intrinsic property of grass species (Serebrjakova 1971).

In this paper the leaves were considered as representatives of basic structural units of a grass organism. Particularly, the leaf blade parameters were studied. Several comparative studies of leaf demography in vascular plants have been published (Sydes 1984; Mitchley 1988; Diemer et al. 1992; Craine et al. 1999) and the methodology of leaf observation has been discussed (Hendry & Grime 1993). Concerning the leaf demography in grasses, attention has been focused mostly on cereals and economically important grasses of productive grasslands (e.g. van Loo 1994; Ryser & Urbas 2000; other references in Serebrjakova, 1971). The xerophytic and steppe grasses were rarely studied in this respect (e.g. Reekie & Redmann 1991; Pugnaire & Haase 1996; Haase et al. 1999; Casper et al. 2001) although considerable work has been devoted to investigations of their life cy-

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

	Poo-Festucetum	*Festuco-Caricetum*
Altitude (m)	380	382
Aspect (°)	180	105
Slope (°)	28	6
Soil/scree 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})	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 of both herb and moss layer (%)	20	70

cles (the bibliography published by Rabotnov 1980, 1981).

The aim of this paper was to assess the basic leaf blade parameters of *Festuca pallens* including natality, mortality, growth, size distribution and life span, and to compare them with the related grass species. Leaf samples of the studied species were studied in the natural environment. Two types of dry grasslands were used as the background of the study as they represent two contrasting environmental conditions. Leaf 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 leaves. Leaf demography in relation to tiller development was also investigated and discussed even though the tiller demography of *Festuca pallens* was particularly described elsewhere (Janišová 2006).

Material and methods

Festuca pallens Host is a perennial polycarpic caespitose grass with a persistent root system and intravaginal tillers without rhizomes. It has a submediterrean-subatlantic distribution in Europe (Hegi 1998). In the West Carpathians *Festuca pallens* inhabits steep and sunny rocks or slopes with shallow rocky neutral to alkaline soils. It is a characteristic species of the alliance *Seslerio-Festucion pallentis* Klika 1931 corr. Zólyomi 1966 where it belongs to the earliest colonisers and dominants (Hegi 1998).

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 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 & Kolbek, 1993). The abbreviated names *Poo-Festucetum* and *Festuco-Caricetum* will be used below. The studied grassland sites have not been managed for at least 25 years.

The permanent plot in the *Poo-Festucetum* was located on a steep strongly eroded south-facing slope covered mostly by dolomite outcrops and scree (Table 1). Due to the slope and low biomass production the soil cover has not been developed. The vegetation covers about 20% and is dominated by *Festuca pallens*. Other relatively abundant species are *Thymus praecox*, *Draba lasiocarpa*, *Teucrium montanum* and *Alyssum montanum*. The cover of cryptogams varies significantly during the year reaching the 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). The soil is shallow and stony but builds more or less continuous layer. Vegetation covers about 70%. *Festuca pallens* and *Carex humilis* dominate in 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*, *Teucrium montanum*, *Potentilla arenaria*, *Globularia punctata*, *Helianthemum grandiflorum* subsp. *obscurum* and *Sanguisorba minor*.

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. The youngest leaf in each tiller was marked for observation. Leaf and tiller characteristics were recorded at three week intervals during the growing season 1993. Only the leaf blade parameters were studied in detail. The group of marked leaves was regarded to be the ML leaf cohort. All leaf cohorts in a tiller were named according to their position on tiller related to the marked leaves (ML). Cohort of leaves one order older was noted as OL, two orders older as OOL, three orders older as OOOL and four orders older as OOOOL. Similarly, leaves of younger cohorts than the marked leaves were noted as YL, YYL, YYYL and YYYYL. Number of living and dead leaves in a tiller was recorded at each recording. 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 (OL, ML and YL) was measured to the nearest millimeter. In length comparison of various leaf cohorts the final length of a leaf blade after its growth has ceased was used for analyses. Damaged leaves (5% in the *Poo-Festucetum* and 25% in the *Festuco-Caricetum*) were excluded from the analyses. At each recording the phenological status of marked leaves was estimated (completely green and growing, yellow at the top, up to 50% dry, more than 50% dry, completely dry). Leaf half-life was determined as the time when 50% of the leaves in a leaf cohort had died.

For a quantitative assessment of leaf turnover, the birth rate (R_b) and death rate (R_d) were calculated at each record date by the formula $R_\mathrm{b} = B/(n \cdot N_t)$, where B is the number of births during n days of an observation period, and

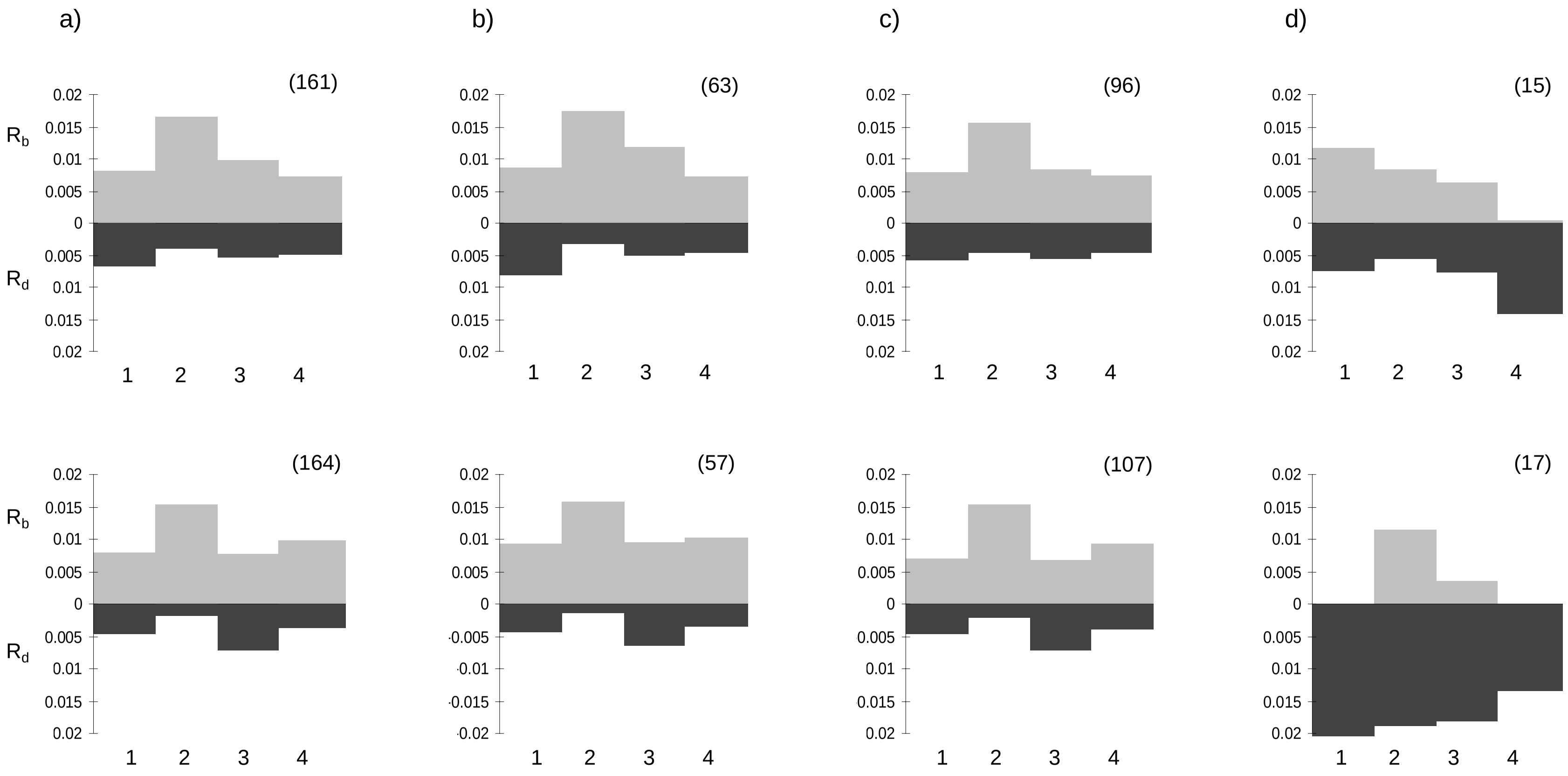

Fig. 1. Leaf turnover in the *Poo-Festucetum* population (upper row) and the *Festuco-Caricetum* population (lower row). Birth rates (R_b, light bars, leaves per tiller per day) and death rates (R_d, dark bars) are shown for tillers a) surviving over the whole observation period, b) surviving and producing daughter tillers, c) surviving without daughter tillers and d) dying during the observation period. Numbers 1–4 show time periods: 1 – May 16–June 6, 2 – June 6–June 28, 3 – June 28–July 21, 4 – July 21–Sept 16. Numbers in parentheses show the amount of tillers on which the diagram is based.

Table 2. Proportion of living leaves in leaf cohorts and mean number of living leaves per tiller during the observation period. In leaf cohorts older than the ML (OL–OOOOL) percentage of surviving leaves is shown. In younger leaf cohorts (YL–YYYYYL) the proportion of tillers that have produced a leaf before the given date is shown. a) *Poo-Festucetum*, b) *Festuco-Caricetum*.

a)

Date	May 16	June 6	June 28	July 21	Sept. 16
YYYYYL	–	–	–	–	6
YYYYL	–	–	–	1	28
YYYL	–	–	1	13	75
YYL	–	–	21	65	94
YL	–	40	92	99	99
ML	100	99	98	95	68
OL	100	93	85	57	0
OOL	51	24	9	4	0
OOOL	8	3	2	0	0
OOOOL	1	1	0	0	0
Number of cohorts with living leaves	5	6	7	7	6
Mean number of living leaves per tiller	2.57	2.58	3.06	3.27	3.42

b)

Date	May 19	June 9	June 29	July 21	Sept. 16
YYYYYL	–	–	–	–	2
YYYYL	–	–	–	–	24
YYYL	–	–	–	2	71
YYL	–	–	10	46	96
YL	–	34	93	100	100
ML	100	99	99	98	77
OL	100	93	86	42	2
OOL	26	9	5	1	0
OOOL	0	0	0	0	0
OOOOL	0	0	0	0	0
Number of cohorts with living leaves	3	4	5	6	7
Mean number of living leaves per tiller	2.24	2.26	2.78	2.70	3.36

N_t is the number of leaves at the beginning of this observation period. Analogously, death rate was calculated: $R_{\mathrm{d}} = D/(n \cdot N_t)$, where D is the number of deaths during n days of an observation period. For evaluation of net gain or loss of leaves the Birth-Mortality Difference (BMD) was calculated: $BMD = R_{\mathrm{B}} - R_{\mathrm{D}}$ (Fig. 1).

Tillers that have survived the whole observation period and tillers that have died before September 1993 were analysed separately to distinguish the effect of tiller death on leaf turnover. The surviving tillers were divided in two groups – tillers that produced daughter tillers during the observation period and those that remained without daughter tillers. The groups were analysed separately to investigate the possible correlation between tillering and leaf demography.

The nomenclature of vascular plant species was unified according to Marhold & Hindák (1998).

Results

Leaf natality and mortality patterns

Although *Festuca pallens* showed little variation in mean number of living leaves per tiller (Table 2) there was a clear variation in both leaf birth and death rates during the observation period. For tillers surviving the whole observation period the course of leaf natality and mortality was similar in both populations (Fig. 1). The highest leaf birth rates and the lowest leaf death rates were observed in June. The birth rates during this period were about twice as high as during the other periods. The birth rates in May, July and August-September were similar. Leaf mortality was much more uniformly distributed in time without a distinct minimum or maximum.

Tillers that died before September 1993 behaved differently. Their birth rates gradually declined and their death rates culminated either at the beginning or at the end of observation period.

For the surviving tillers the leaf production exceeded the leaf mortality during the whole observation period (Table 3). The highest net gains were achieved in June. As expected, tillers that died showed either a steady decrease of net gain or a permanent loss.

Leaf demography and tiller survival

In both populations the surviving tillers had higher leaf birth rates than dying tillers during the whole growing season, but these differences were highly significant only in August-September period (Table 4). The leaf death rates were higher for the dying tillers during the whole growing season. In the *Festuco-Caricetum* pop-

Table 3. Birth-Mortality Differences evaluating the net gain or loss of leaves calculated for surviving and dying tillers.

	May	June	July	August-September
Surviving tillers				
Poo-Festucetum	0.0013	0.0125	0.0043	0.0025
Festuco-Caricetum	0.0032	0.0135	0.0007	0.0059
Dying tillers				
Poo-Festucetum	0.0042	0.0028	−0.0014	−0.0138
Festuco-Caricetum	−0.0215	−0.0076	−0.0145	−0.0134

Table 4. Leaf demography and tiller survival. Differences of leaf birth and death rates between the surviving (S) and dying (D) tillers tested by the Mann-Whitney test.

Leaf characteristic	Time period	*Poo-Festucetum*		*Festuco-Caricetum*	
Birth rate	May	n.s.	$P = 0.2949$	$S > D$	$P = 0.0199$
	June	$S > D$	$P = 0.0345$	n.s.	$P = 0.5028$
	July	n.s.	$P = 0.2059$	n.s.	$P = 0.2858$
	August–September	$S > D$	$P < 0.0001$	$S > D$	$P < 0.0001$
Death rate	May	n.s.	$P = 0.8374$	n.s.	$P = 0.0556$
	June	n.s.	$P = 0.9303$	$S < D$	$P = 0.0251$
	July	n.s.	$P = 0.3879$	$S < D$	$P = 0.0061$
	August–September	$S < D$	$P < 0.0001$	$S < D$	$P < 0.0001$

Table 5. Average length of leaf blade in three leaf cohorts. Mann-Whitney test for differences in means was used for the analysis.

	Poo-Festucetum	*Festuco-Caricetum*	
Maximum leaf length in a tiller	5.96	6.78	$P = 0.0009$
Leaf length of the OL cohort	4.68	4.74	n.s.
Leaf length of the ML cohort	5.49	6.28	$P = 0.0003$
Leaf length of the YL cohort	4.23	4.91	$P = 0.0014$

ulation the significance of these differences increased gradually reaching the highest value in late summer. In the *Poo-Festucetum* population death rates of dying and surviving tillers differed significantly only in the August-September period.

Leaf demography and tillering

There were no significant differences in leaf demography between tillers that produced daughter tillers during the observation period and those remaining without daughter tillers (Mann-Whitney test). The greatest differences (at the border of significance $P = 0.073$ and $P = 0.071$) were revealed in the birth rate during July when the tillers producing daughter tillers had higher leaf birth rates. BMD values were positive during the whole growing season also in the tillers with parallel tillering.

Leaf size

The length of leaf blade in *Festuca pallens* was 7 to 137 mm. In general, leaves of the ML cohort were the longest (average length 59 mm; in comparison to the OL cohort with 47 mm and the YL cohort with 46 mm). There was no difference between the studied populations in leaf length of the OL cohort (Table 5). Leaves of both the ML and the YL cohorts were significantly longer in the population of *Festuco-Caricetum.* The maximum length of leaf blade in a tiller was higher in the *Festuco-Caricetum*, too.

Growth, increments and seasonal aspects

The leaves grew during the whole year. The winter cold and summer drought might slow down or interrupt the growth. Growth intensity of the ML cohort was expressed by average daily increments (Table 6). Daily leaf increments during May and June were higher in the *Festuco-Caricetum* (Mann-Whitney test, $P = 0.0074$ and $P = 0.0004$). There were no differences between the populations in leaf increments during later periods. Following the trend of leaf growth, 50% of the leaves in the ML cohort stopped growing after about one month (28.5 days in the *Poo-Festucetum* and 28 days in the *Festuco-Caricetum*). The last leaf in the cohort ceased its growth after 57 days in the *Poo-Festucetum* and 56 days in the *Festuco-Caricetum.*

Leaf senescence and life span

The gradual leaf senescence of the ML cohort is shown in Fig. 2. The proportion of leaves with green apex gradually decreased to the detriment of yellowing and dead

Table 6. Daily leaf increments of the ML cohort during the observation period in a) *Poo-Festucetum*, b) *Festuco-Caricetum*.

a)

Time period	May 16–June 6	June 6–June 28	June 28–July 21	July 21–Sept 16
Number of growing leaves	151	120	48	2
% of the whole sample ($n = 163$)	93	74	29	1
Average daily increment (mm)	0.53	0.30	0.03	0.00

b)

Time period	May 19–June 9	June 9–June 29	June 29–July 21	July 21–Sept 16
Number of growing leaves	124	116	44	2
% of the whole sample ($n = 129$)	96	90	34	2
Average daily increment (mm)	0.67	0.43	0.04	0.00

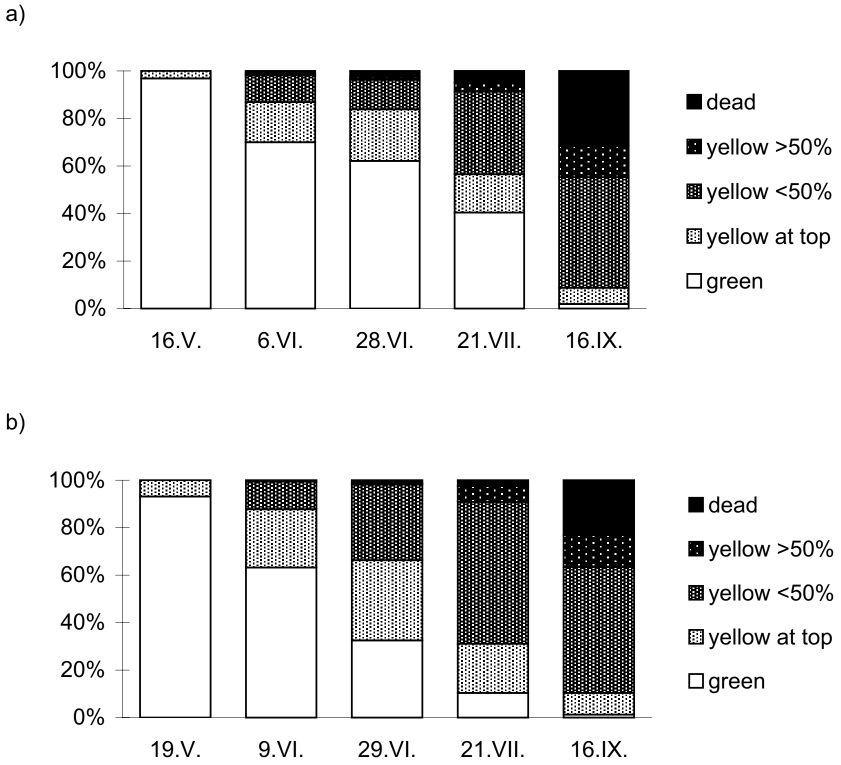

Fig. 2. Leaf senescence of the ML cohort in the population of a) *Poo-Festucetum* and b) *Festuco-Caricetum*. Proportion of leaves in various phenological status is shown at five recording dates in 1993: completely green leaves (triangles), leaves green up to 50% (quadrates), leaves with at least some green parts (circles). Only leaves on tillers surviving the whole observation period are included.

leaves. This process had a similar trend in both studied populations and was only slightly faster in the *Festuco-Caricetum*.

The process of leaf senescence seems to be accelerated during later periods of leaf life as it can be seen from the Fig. 3 showing the survivorship curves of leaf cohorts older than the ML cohort. Here the leaf survival followed the general trend: high and stable survival (plateau) at the beginning, slight decline in survival during the later period, remarkable decline in survival followed by a prolonged tail.

Leaf life span was estimated by the analysis of survivorship curves of the ML cohort (Fig. 4). If leaf life span was measured to the moment when the last green part of a leaf loses its ability for photosynthesis, the uppermost curve (circles) shows the leaf survival. Then, about a quarter of the leaves died until September. The leaf half-life would take about 150–200 days. The life span of an average leaf could exceed half a year.

The number of cohorts containing living leaves increased during the recorded time (Table 2) reaching its maximum in July in the *Poo-Festucetum* and in August-September in the *Festuco-Caricetum*. Number of living assimilating leaves per tiller increased progressively during the growing season and the variance of data increased simultaneously. At all recording

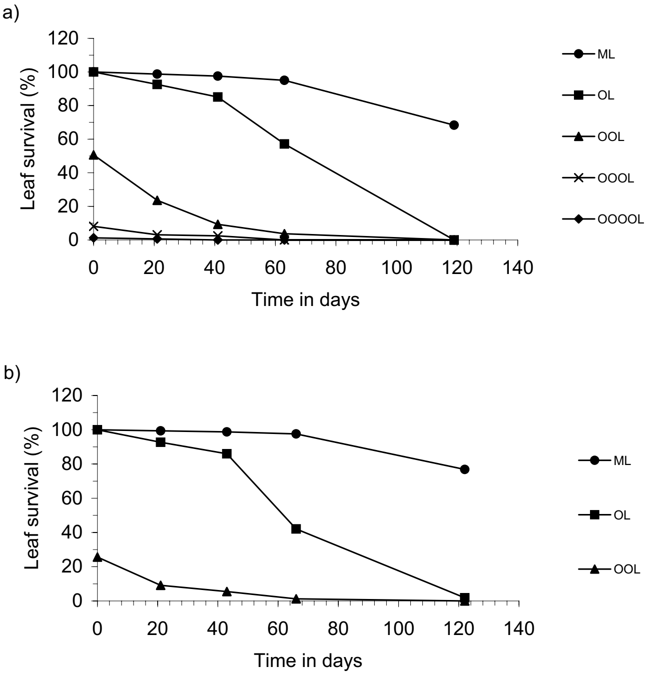

Fig. 3. Survival of various leaf cohorts during the observation period in a) *Poo-Festucetum* and b) *Festuco-Caricetum*. ML – cohort of the marked leaves, OL – cohort of leaves one order older than the marked leaves, OOL – cohort of leaves two orders older, OOOL – cohort of leaves three orders older, OOOOL – cohort of leaves four orders older.

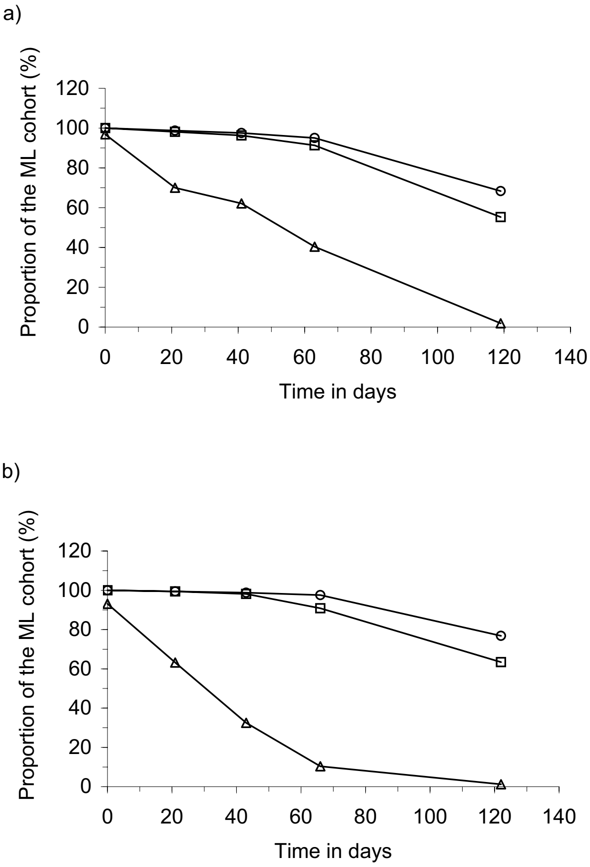

Fig. 4. Survival and senescence of the ML cohort in a) *Poo-Festucetum* and b) *Festuco-Caricetum*. Only leaves on tillers surviving the whole observation period are included. Three curves are shown for each population expressing the proportion of completely green unharmed leaves (triangles), leaves green up to 50% (quadrates) and leaves with at least some green parts (circles).

times except the last one, the mean values in the *Poo-Festucetum* population were significantly larger than in the *Festuco-Caricetum* population (t-test, $P < 0.001$).

Discussion

Leaf natality and mortality patterns

In comparison to other grasses and graminoids *Festuca pallens* shows relatively low rate of leaf turnover. Mitchley (1988) found the slowest turnover in *Avenula pratense* and *Bromus erectus*. Their values of R_b and R_d fluctuated between 0.01 and 0.05 leaves per tiller per day. In *Festuca pallens* this was only 0.0019 and 0.0165 (surviving tillers).

The steady net gain of leaves in both populations was not interrupted even by the parallel process of tillering, which is otherwise common (e.g. Bazzaz & Harper 1977; van Loo 1993). The effects of flowering and seed ripening on leaf demography cannot be evaluated for *Festuca pallens* as only vegetative tillers were observed. The direct consequence of permanent net gain of leaves during the growing season is a gradual increase in number of living leaves per tiller and its culmination at the end of the growing season. The high leaf life span (about half a year) seems to play a significant role as well. Leaf birth rate probably declines during autumn and winter while the leaf mortality increases. The accumulated leaves gradually get old and the number of living leaves falls to its minimum at the end of the winter.

A certain phenological pattern determined by cycles of leaf natality and mortality has been found for graminoids (Mitchley 1988), and can be seen also in the *Festuca pallens* diagrams. According to Mitchley (1988) the graminoid tiller is a more invariant module than the dicotyledonous rosette, and after the production of three or four leaves per tiller, the birth of a new leaf tends to be accompanied by the death of an old one.

Slight increase in mortality at the beginning of the observation period (May) might be due to natural death of one of the overwintering leaf cohorts. This has also been seen in *Globularia punctata* (Hiebinger & Mucina, unpublished data) and in *Carex subspathacea* (Kotanen & Jefferies 1987). The higher mortality in July can be a consequence of high temperatures and drought.

Leaf demography and tiller survival

Tillers that died during the observation period differed from those that survived by increased leaf mortality rather than by a declining leaf production. A highly significant decrease in leaf natality occurs earliest in late summer (differences of lower significance were found also during May in the *Festuco-Caricetum* and during June in the *Poo-Festucetum*).

Leaf demography and tillering

The process of tillering sometimes affects leaf length (van Loo, 1993) and leaf production (Hiebinger & Mucina, unpublished data). This was not seen in our data. Furthermore, in *Festuca pallens* the development of axillary buds into daughter tillers as a parallel process of tiller apical growth did not restrict basic demographic processes such as leaf birth and death. Actually, tillers that produce daughter tillers seem to have higher leaf birth rates although these differences are only at the border of statistical significance.

Leaf size

The gradual change of leaf length related to the leaf position on a tiller is a generally accepted phenomenon (e.g. Gogina 1961; Serebrjakova 1971; Holmes 1989). In the tillers of *Festuca pallens* the ML cohort produced in May achieved the greatest length of leaf blades.

Comparing the leaf length of three leaf cohorts (OL, ML, YL) it is important to realise that the differences between the studied populations may be due to the shift in the phenological development in their habitats (e.g. earlier beginning of the growing season at southern slopes). Thus the leaves although measured in the same time in both populations might belong to phytomers of various orders and differ as a consequence of intrinsic leaf length graduation within a tiller.

Besides the phenological shift between the studied populations several possible explanations of differences in leaf length are available. The leaf length is regarded as a consequence of growth processes determined by external and internal regulation. Its variability can be induced by several factors: leaf position on a tiller, tiller age, genetic disposition or environmental factors. Significant differences in the leaf length between the studied populations were detected only for the May (ML) and June (YL) leaf cohorts. This suggests that they are determined by an environmental factor with a seasonal effect such as the temperature- and water-regime of the habitat. Drought is often restricting the final leaf length (e.g. Holmes 1989 for grasses in general; Hroudová-Pučelíková 1972 for *Festuca rupicola* and *F. valesiaca*; Willms 1988 for *Festuca scabrella*).

Leaf senescence and life span

Slightly faster leaf senescence in the *Festuco-Caricetum* population can be due either to age differences between leaf samples (marked leaves in the *Festuco-Caricetum* might have been older) or to the increased disturbances during summer months recorded in the *Festuco-Caricetum* (about 25% of leaves marked for observation were harmed here opposite to 5% in the *Poo-Festucetum*).

If we compare the values of life span in several grass species we always have to consider the methods of its estimation (concerning the definition of leaf birth, leaf death and leaf life span). Hendry & Grime (1993) defined the longevity of a leaf as the time from a leaf becoming discernible to the time of senescence, when more than 75% was no longer green. Mitchley (1988) defined leaf birth as the time at which the leaf bud was first observed and leaf death as the time at which more than 90% of the laminar tissue was dead. Thus the comparison is reasonable with our data considering leaves as alive although they get yellow and loose most of their photosynthetic capacity (Fig. 4). Our estimates of *Festuca pallens* leaf life span (half-life about 150–200 days) were based on the preposition that a leaf is alive until the complete loss of its photosynthetic ability. Considering the curve showing the number of leaves green at least to 50% as leaf survivorship curve, the estimated leaf life span would be shorter, the half-life reaching about 130–150 days.

Comparisons with the published literature show that *Festuca pallens* belongs to the species with very long-lived leaves. The estimated value of its leaf half-life (150–200 days) was higher than in any other grass species published. The grasses with the longest leaf life span (in days) are the following: *Avenula pratensis* (127, Mitchley 1988), *A. pubescens* (103, Ryser & Urbas 2000), *Briza media* (102, Mitchley 1988 and 113, Ryser & Urbas 2000), *Deschampsia cespitosa* (113, Ryser & Urbas 2000) and *Melica nutans* (111, Ryser & Urbas 2000). Higher estimate of leaf life span was found only in sedge *Carex flacca* (190, Mitchley 1988). On the other hand, fast growing perennial grasses with broad leaves e.g. *Arrhenatherum elatius*, *Festuca pratensis*, *Holcus lanatus*, *Lolium perenne* and *Poa trivialis* have short-lived leaves with life spans of about 30 to 45 days (Sydes 1984; Diemer et al. 1992; Hendry & Grime 1993; Ryser & Urbas 2000). Annual grasses such as *Alopecurus myosuroides*, *Bromus hordeaceus*, *B. sterilis*, *B. tectorum* and *Poa annua* have the shortest leaf life span from 19 to 29 days (Ryser & Urbas 2000).

Leaf life span is probably related to investment in leaf structure and size (Chabot & Hicks 1982; Chapin 1989; Hendry & Grime 1993) so that the leaves with very substantial leaf structure and sclerophylly tend to live long. Slow growth rates and long life span in narrow-leaf grasses is related to their long-term success in nutritionally poor habitats (Grime 1979; Ryser & Urbas 2000). These adaptations restrict the loss of nutrients from both plants and their habitats. This fits our results on *Festuca pallens* leaf demography.

Leaf life span is undoubtedly important in “foraging for light” (Hendry & Grime 1993). The exploitation of a dynamic patchwork of irradiance is aided by a high turnover (i.e. short life-span) of leaves. Thus a permanent intensive irradiance in the studied dry grasslands together with the above mentioned high investment in the sclerophyllous leaf structure can be considered as the two main factors inducing the long life span of leaves in *Festuca pallens*.

According to Mitchley (1988) there were only slight differences in the values of leaf life span and half-life between the various monthly cohorts and there was no obvious trend or fluctuation in these values. In our study of *Festuca pallens* the life span estimated for the ML cohort is therefore supposed to be valid for leaves in general. However, the turnover of leaves in the juvenile and adult stages of plant development can differ and this relationship needs to be examined (Hendry & Grime 1993).

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