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Tiller dynamics of two grasses – responses to grazing, density and weather

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Summary

1 The tiller dynamics of the two dominant species in a grassland, *Agrostis stolonifera* and *Lolium perenne*, were followed for two years in a field grazing experiment. Sheep grazing was applied in three seasons at two grazing intensities; winter, spring (in both seasons grazed or ungrazed) and summer (hard or light grazed).

2 Tiller densities of both species showed peaks in late summer and troughs in spring due to variation in tiller birth rates. Tiller death rates were not seasonal. Year-to-year weather variation also affected the dynamics.

3 Harder summer grazing increased tiller birth and death rates of both species, increasing tiller turnover, but did not affect tiller densities. The tiller death rates were higher and the summer peak in birth rates was earlier in the winter-grazed paddocks. Therefore, winter grazing decreased tiller densities over the two years by reducing densities in the non winter-grazed paddocks during the late summer months. There were no main effects of spring grazing treatment or interactions among grazing treatments. Tiller birth and death rates were density-dependent, indicating that the populations were regulated.

4 *Agrostis* generally had higher tiller birth and death rates and therefore had a more rapid tiller turnover than *Lolium*. Fewer tillers flowered and there was less seedling establishment in the *Agrostis* populations. However, both species showed similar seasonal dynamics, density-dependent regulation, effects of between year climatic variation and responses to spring and summer grazing treatments. *Agrostis* showed a significantly greater response to winter grazing.

5 The tiller populations of both species were regulated by density-dependent birth and death rates but showed seasonal dynamics upon which were superimposed effects of grazing treatment and yearly variation in the weather. However, their tiller population numbers were little affected by grazing level in spring or summer. Only grazing in winter decreased their densities and this is the treatment most likely to bring about changes in species composition in the grassland.

Keywords: *Agrostis stolonifera*, density-dependence, *Lolium perenne*, seasonal dynamics, sheep grazing

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Introduction

Vertebrate grazing is a major influence on the species composition of grassland communities. Two complementary aspects of this grass–grazer interaction are of fundamental interest: how alterations in grazing regime or intensity may alter species composition (e.g. Bakker 1989) and how stability of grassland com-

position is achieved (e.g. Noy-Meir 1975). The key to understanding both of these processes lies in how the grazing regime affects the population dynamics of grassland plants. Grass tiller turnover rates are high outside habitats with extremes of low temperature or rainfall (Jonsdottir 1991; L'Huillier 1987; Tallowin *et al.* 1989), and therefore their populations have the potential for rapid change in response to environmental change. If grazing affects rates of net tiller replacement in different species differently, the relative abundance of species may change quite quickly. Conversely, high tiller turnover permits a rapid

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replacement of plants lost to herbivores, providing the potential to stabilize species composition.

In this paper we report a detailed study of the tiller dynamics of the grasses *Lolium perenne* and *Agrostis stolonifera* in a species-poor temperate grassland where they were the two most abundant plant species. The study was conducted inside a replicated sheep grazing experiment, which provided the opportunity to establish whether grazing treatments affected the dynamics of the two species differently. Previous studies at this site have found that grazing treatments did significantly affect the abundance of grass and dicot species, although the overall changes to the plant community in the first five years of the grazing experiment were slight (Bullock *et al.* 1994; Treweek 1990). This suggests that the plant community at our site is stable and highly resistant to change (Silvertown *et al.* 1992). The key to the stability of the community is most likely to lie in the dynamics of its two dominant species. The main source of perturbation in the dynamics of the dominant grasses is grazing, but we also report the effects of season and yearly variation in weather and test for density-dependent population-regulating factors.

Methods and materials

SITE DESCRIPTION

The grazing experiment was set up at Little Wittenham Nature Reserve in Oxfordshire, England (National Grid reference US568924) in 1986 (Treweek 1990). The site is on the Berkshire Downs and the soil is a calcareous clay loam. Cultivation last occurred in the 1940s and subsequently the site was seeded with an agricultural grass mix and managed with sheep grazing and fertiliser application. All application of chemicals was ceased in 1984 (Tennyson 1992). The sward was species poor and dominated by agricultural grasses (Bullock *et al.* 1994) and was in the MG7 category of the National Vegetation Classification (Rodwell 1992).

Grazing treatments were applied in three seasons: 'winter' (1 November – 21 March), 'spring' (21 March – 21 May) and 'summer' (21 May – 1 November). Within each season there were two levels of grazing. In winter and spring paddocks were ungrazed or grazed by two Suffolk × Mule ewes per paddock and in summer the sward height was maintained at either 3 cm or 9 cm by weekly measurement of the sward height followed by adjustment of the stocking rate. The experiment was fully factorial with a $2 \times 2 \times 2$ structure and two randomised blocks assigned over 16 (2×8) 50-m × 50-m paddocks (Table 1). This design allowed analysis of results by three-way ANOVA of a variable to determine the main effects, i.e. grazing level in a season, and interaction effects of the grazing levels in the three seasons.

Table 1 Design of the grazing experiment. A minus sign indicates no grazing and a plus sign indicates grazing during the relevant period. All paddocks were grazed in summer to either 3 cm or 9 cm in height. The treatments were arranged in two blocks.

Treatment	Winter	Spring
Summer 3 cm		
A	–	–
B	–	+
C	+	–
D	+	+
Summer 9 cm		
E	–	–
F	–	+
G	+	–
H	+	+

TILLER DYNAMICS

On 14 March 1990 four sites were randomly selected in each of the 16 paddocks, avoiding a boundary strip of 10 m around the perimeter of each paddock to reduce edge effects. At each site a 10-cm × 10-cm stainless-steel wire quadrat was fixed with wire pins flush to the soil surface. Two sites were assigned to *Lolium perenne* and two to *Agrostis stolonifera* and if no tillers of the target species were found in the initial inspection the quadrat was moved to a new random location. Such relocation was rarely necessary. The quadrats were first censused on 3–5 April 1990. All tillers of the target species rooted within the quadrat were counted and marked at the base with a spot of nontoxic acrylic colour poster paint. Only tillers at or beyond the first leaf stage were marked. Censuses were carried out in the first week of each calendar month until April 1992 inclusive, except in January, February and June 1991 when poor weather prevented censusing. At each census a new colour of paint was used to mark the new cohort of tillers and the surviving tillers of each cohort were counted. Most tillers were of clonal origin and any seedlings were marked with a different colour and their fates were followed separately from the clonal cohorts. Flowering tillers were counted and marked to indicate date of flowering.

ANALYSIS

The sheep grazing experiment was designed so that the effects on a variable of the two grazing levels in each season could be analysed in a $2 \times 2 \times 2$ ANOVA. This structure was extended into a three-stratum split-plot structure to allow the effects of species and census date to be determined. The blocks and grazing treatments were on the first stratum. The second stratum represented the four quadrats in each paddock and therefore contained the sources of variation due to the two species and to the two replicate quadrats. The species were considered as treatments so that their

differences could be determined within the ANOVA structure. The replicate quadrats were considered separately in the ANOVA to allow the effects of density on the variables to be analysed. The third stratum contained the variation within each quadrat among the censuses. The ANOVA model described the main and all interaction effects of every factor except the blocks and replicates which were analysed as main effects only. The third stratum consisted of repeated measures of individual quadrats and thus violated the ANOVA assumption of independent measures. This can be overcome by a variety of statistical methods (France *et al.* 1986; Maxwell & Delaney 1990) and the one chosen allowed us to retain the split-plot ANOVA model. This involved the calculation of Box's $\hat{\epsilon}$, a statistic measuring the departure of the population covariance matrix from homogeneity (Maxwell & Delaney 1990, pp. 475–479). The degrees of freedom for the ANOVA of the census stratum were multiplied by the estimated $\hat{\epsilon}$ and used to determine a new and increased critical value for F which was compared to the F -values derived from the split-plot ANOVA. Perfect homogeneity would give an $\hat{\epsilon}$ of one, but the $\hat{\epsilon}$ values were all less than one, causing an increase in the critical F -value.

The density of tillers per quadrat varied with every factor and because of the possible effects of density on tiller dynamics it was necessary to ascertain and control for the effects of density within the analysis. This was done by adding in the density of tillers in the previous census as a covariate at every stratum of the ANOVA.

Results

RELATIVE TILLER DENSITIES

Over the two year period the fates were followed of 9048 *Lolium* tillers and 10 221 *Agrostis* tillers. Because there were very few seedlings these were unimportant in the tiller dynamics. Seedling dynamics are considered separately below.

The initial density of tillers per quadrat in April 1990 (mean = 54.6) showed no treatment effects except a significant summer–spring–winter–grazing interaction ($F = 5.68$, $P < 0.05$). Initial tiller densities ranged from 9 to 200 per quadrat and therefore treatment effects were analysed as the changes in tiller density over time as a percentage of the initial density in each quadrat. Table 2 shows the results of the split-plot ANOVA on this variable and these are described below. Relative density varied significantly among the censuses for both species with the mean final density in April 1992 (mean = 45.4) being less than the initial density. This variation appeared to be seasonal (Fig. 1a) with tiller density peaking in the late summer (August–October) and showing troughs in the spring (March and April). These increases and decreases coincided with the those of the mean temperature in

the month previous to the census date (Fig. 2) and a regression analysis showed a significant positive correlation between mean monthly maximum temperature and the relative tiller density ($r = 0.74$, $n = 22$, $P < 0.01$).

In all censuses after April 1990 *Agrostis* had significantly higher tiller densities than *Lolium* (Fig. 1a). The seasonal variation in mean density was also greater in *Agrostis* (90.2–172.2%) than in *Lolium* (75.8–120.7%). Winter grazing decreased tiller densities of both species but this effect evolved over time, creating a census–winter–grazing interaction (Fig. 1b,c). For both species, tiller densities were similar in both winter grazing treatments from the start of monitoring until the September 1990 census when tiller densities increased most in the non-winter-grazed paddocks and stayed higher in these paddocks for the remainder of the censuses. The winter grazing effect also varied between the species, resulting in a significant census–species–winter–grazing interaction. Both species had increased tiller densities in the non winter-grazed paddocks after September 1990, but, whereas this effect remained stable over time for *Lolium* (Fig. 1b), *Agrostis* exhibited an increased divergence between the two treatments from July 1991 which continued throughout the remaining census period (Fig. 1c). Although the two species in both treatments showed the seasonal fluctuations in tiller densities, a comparison of the two years shows that superimposed on this seasonal effect were decreases in tiller densities in winter grazing and increases in non winter-grazed paddocks in the second year compared to the first. This effect was much larger for *Agrostis* and therefore, by the end of the monitoring, the species differences in tiller density were large in the non winter-grazed paddocks but had disappeared in winter-grazed paddocks. For this reason an ANOVA on the percentage change in tiller density between April 1990 and April 1992 showed winter-grazing ($F = 13.49$, $P < 0.01$) and species–winter–grazing ($F = 8.97$, $P < 0.01$) effects.

CHANGE BETWEEN CENSUSES

Further analyses were carried out to discover the processes by which the treatments affected tiller densities. The change in tiller density between each census as a percentage of the density at the previous census was calculated for each quadrat at each census and a split-plot ANOVA showed a number of treatment effects on this variable (Table 2). For both species the percentage change varied significantly among censuses (Fig. 3a), with a succession of positive changes in density through the late spring and summer and negative changes throughout the autumn and winter. There were negative changes in tiller density in the July and August 1990 censuses probably because of a severe drought in this summer (rainfall from May to September 1990 was 45% of the 1951–91 local average, but the corresponding percentage for 1991 was

Table 2 The results of split-plot ANOVA on the derived variables. All variables showed homogeneity of variance. Winter, Spring and Summer are abbreviations for grazing effects in those grazing seasons. Only some of the main and interaction effects are shown, those not shown were nonsignificant. The degrees of freedom for each effect are shown. The $\hat{\epsilon}$ values which modify the critical F -value in the third stratum are given. For three of the variables the density at the previous census was added as a covariate and its effect is shown. When the covariate was added the denominator degrees of freedom were decreased by one

Stratum	Factor (d.f.)	Relative tiller number	Percentage change between censuses	Daily tiller birth rate	Daily tiller death rate
Stratum 1	winter (1,7)	11.83**	22.26**	0.05	6.86*
	spring (1,7)	0.03	0.86	0.04	0.33
	summer (1,7)	0.00	0.00	6.87*	8.77*
	density (1,6)	X	0.10	1.79	4.44
Stratum 2	species (1,23)	4.65*	12.23**	188.93***	75.53***
	density (1,22)	X	0.15	0.54	1.10
Stratum 3	$\hat{\epsilon}$	0.255	0.417	0.387	0.561
	census (20,959)	8.36***	13.91***	13.78***	11.65***
	census \times species (20,959)	1.99	2.44*	2.92**	2.27**
	census \times winter (20,959)	7.97***	4.22**	4.73***	2.45**
	census \times spring (20,959)	1.35	1.89	1.50	1.35
	census \times summer (20,959)	0.57	1.44	1.87	1.17
	census \times species \times winter (20,959)	3.60**	2.26*	2.79***	1.27
	density (1,958)	X	60.78***	35.87***	45.45***
	Others	summer \times winter $F_{1,6}$	6.04*	—	—

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

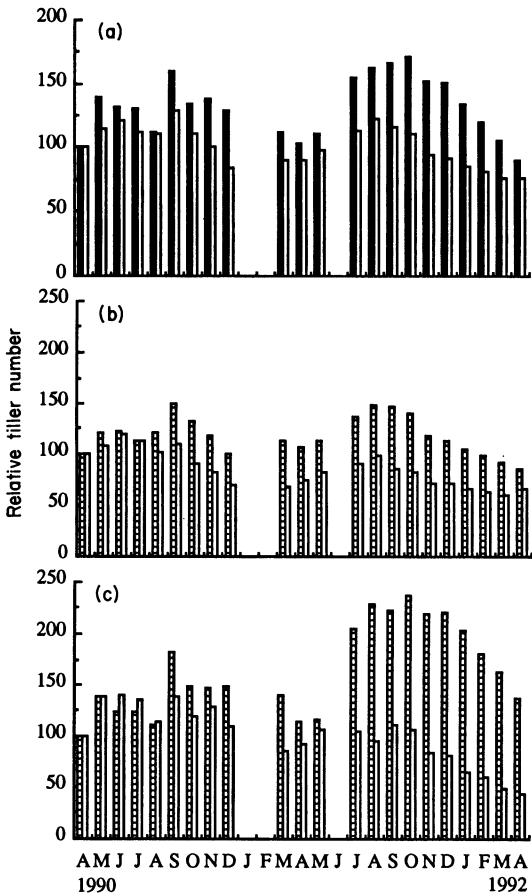


Fig. 1 Relative tiller numbers from April 1990 to April 1992 under different treatments. Tillers numbers are given as a percentage of the initial numbers. (a) Each species pooled over the grazing treatments: ■, *Agrostis stolonifera* and (□) *Lolium perenne*. Winter grazing effects on (b) *Lolium perenne* and (c) *Agrostis stolonifera*: □, non-winter-grazed; ■, winter-grazed.

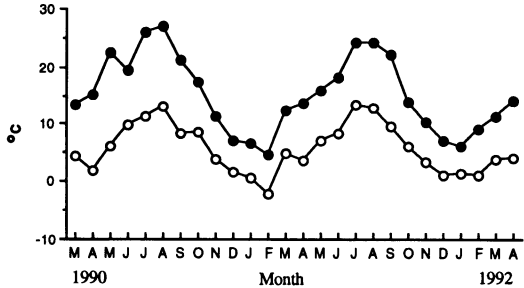


Fig. 2 Mean daily maximum temperature (●) and the mean daily minimum temperature (○) at Little Wittenham Nature Reserve from March 1990 to April 1992.

117%). Because the changes between monthly censuses were so marked the missed censuses in January, February and June 1991 caused a real loss of data about the dynamics of the system. Extrapolating the data however, indicates that it is likely that tiller densities fell or remained constant during January and February and increased in June.

There was a census–species interaction effect on percentage change (Table 2). Separate ANOVAS for each census showed that this was because the species had significantly different percentage changes at three censuses only, namely May 1990, September 1990 and July 1991 (Fig. 3a). These were the dates of greatest increase in tiller densities, with *Agrostis* increasing more than *Lolium*.

ANOVAS at each census indicated that the census–winter-grazing interaction arose because there were larger positive percentage changes in the non-winter-grazed paddocks in five censuses, namely August 1990, September 1990, December 1990, July 1991 and August 1991 (Fig. 3b). There was however, a sig-

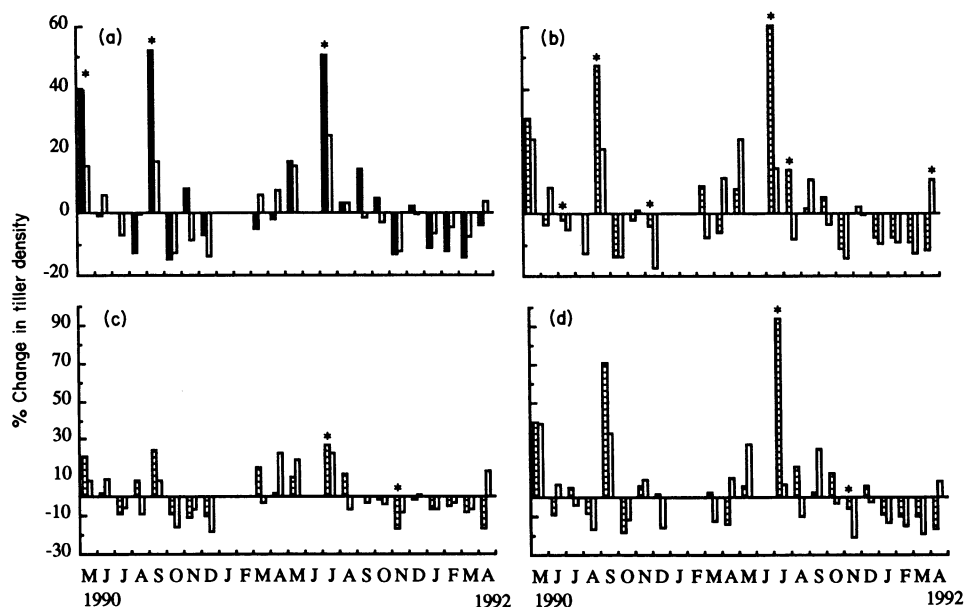


Fig. 3 Percentage change in tiller numbers from May 1990 to April 1992 and the effects of different treatments on this variation. (a) Each species pooled over the grazing treatments. ■, *Agrostis stolonifera*; □, *Lolium perenne*. The asterisked censuses represent significant species differences in separate ANOVAs at each census. (b) The effects of winter grazing pooled over the two species: □, non-winter-grazed; ▤, winter-grazed. The asterisked censuses represent significant winter grazing effects in separate ANOVAs at each census. (c) Winter grazing effects on *Lolium perenne*. Symbols are the same as those in (b). (d) Winter grazing effects on *Agrostis stolonifera*; symbols are as in (b). The asterisked censuses in (c) and (d) represent significant species–winter-grazing interactions in separate ANOVAs at each census.

nificant reversal of this trend in April 1992. The two species showed generally similar responses to the winter grazing treatments (Fig. 3c,d). However, there was a census–species–winter-grazing interaction because there were significant species differences in the response to winter grazing in July and November 1991 (detected by separate ANOVAs at each census), when winter grazing had little effect on *Lolium* but decreased the percentage change of *Agrostis* (Fig. 3c,d).

BIRTH AND DEATH RATES

Birth and death rates of tillers per quadrat were calculated, respectively, as the number of new or dead/missing tillers at a census divided by tiller number at the previous census and the number of days since the last census. The missing of the January, February and June 1991 censuses will therefore have introduced errors into the estimation of rates for the March and July 1991 censuses by the loss of data from tillers which were born and died between the successful censuses and lived over the period of a missed census.

Both birth and death rates varied significantly among the censuses (Table 2) but they showed rather different forms of variation. The birth rates of both species followed a seasonal trend, increasing in summer and decreasing in winter, although rates were very low from June–August 1990 (Fig. 4a). A regression with the mean maximum temperature indicated a weakly significant trend for increasing birth

rate with higher temperatures ($r = 0.40$, $n = 21$, $P = 0.07$). Variation in the death rate showed no seasonal trend (Fig. 5a) and was not correlated with temperature ($r = 0.03$, $n = 21$, not significant). However, despite some interaction effects, the two year time trend of the death rates was fairly consistent between grazing treatments and between the species (Fig. 5a, b).

Both variables showed census–winter-grazing interactions (Table 2). Birth rate showed similar seasonal trends in both winter grazing treatments but individual ANOVAs at each date showed significant increases in birth rate under winter grazing in April 1991, May 1991 and April 1992 and a significant decrease in birth rate under winter grazing in July 1990, August 1990, September 1990, July 1991, August 1991 and December 1991 (Fig. 4b). Winter grazing had a significant main treatment effect on the death rate, increasing mortality in most censuses (Fig. 5b). There was a census–winter-grazing interaction effect on death rates due to occasional reversals of the winter grazing effect and variations in the extent of the grazing effect among censuses, although there were the same time trends in both treatments. Because of these effects, the time trend of the winter grazing effects on the birth rates mirrors the pattern for percentage change almost exactly (Figs 3a and 4a).

The mean birth and death rates were significantly higher in *Agrostis* (0.0096, 0.0086 tillers tiller⁻¹ day⁻¹, respectively) than in *Lolium* (0.0055, 0.0056 tillers tiller⁻¹ day⁻¹, respectively) and they were higher in

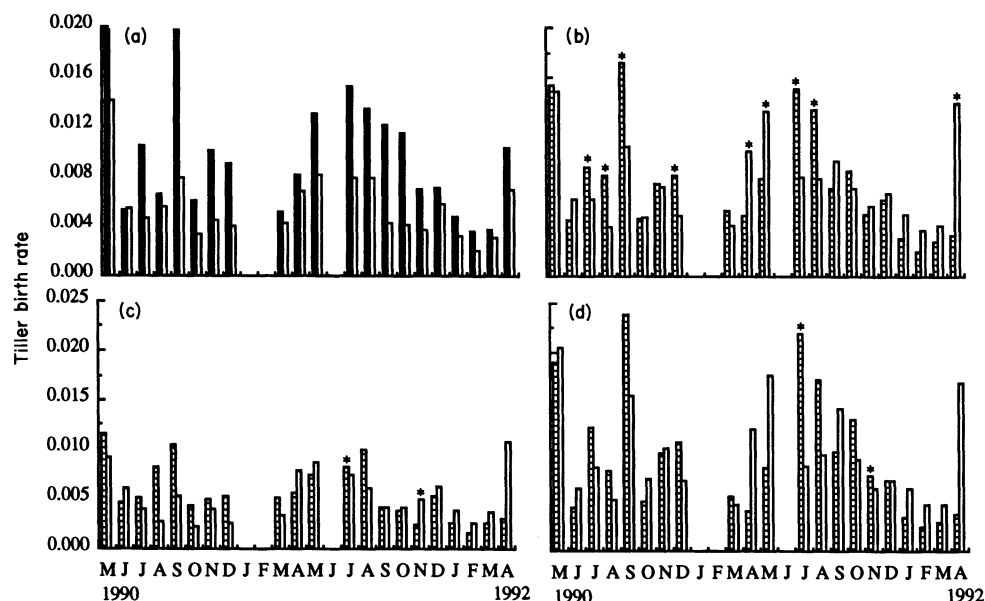


Fig. 4 The birth rate of tillers (tillers tiller⁻¹ day⁻¹) from May 1990 to April 1992 under different treatments. (a) Each species pooled over the grazing treatments: ■, *Agrostis stolonifera*; □, *Lolium perenne*. (b) The effects of winter grazing pooled over the two species: ▨, non-winter-grazed; □, winter-grazed. The asterisked censuses represent significant winter grazing effects in separate ANOVAs at each census. (c) Winter grazing effects on *Lolium perenne*; symbols are as in (b). (d) Winter grazing effects on *Agrostis stolonifera*; symbols are as in (b). The asterisked censuses in (c) and (d) represent significant species–winter-grazing interactions in separate ANOVAs at each census.

Agrostis in almost all the censuses (Figs 4a and 5a). However, both variables showed census–species interactions. The change in species differences among the censuses showed no particular pattern and were caused by wider ranging birth and death rates in *Agrostis* (0.0036–0.0197 and 0.0049–0.0125 tillers tiller⁻¹ day⁻¹, respectively) than *Lolium* (0.0021–0.0105 and 0.0032–0.0092 tillers tiller⁻¹ day⁻¹, respectively). The higher birth and death rates in *Agrostis* cancelled out in most censuses, so the species did not differ in the percentage change in tiller density (see above). However, the species difference was much greater in the birth than the death rates in May 1990, September 1990 and July 1991, causing species differences in the percentage change in these censuses.

Birth rate also showed a census–species–winter-grazing interaction, although individual ANOVAs on each census showed species–winter-grazing effects only in July 1991 and November 1991 (Figs. 4c, d). In these censuses large negative effects of winter grazing on *Agrostis* contrasted with a negligible effect in July 1991 and a reversed effect November 1991 on *Lolium*. These effects explain the species differences in the response of the percentage change of tillers to winter grazing in these two censuses (Fig. 3c,d).

The relative extents to which variation in the birth and death rates could explain variation in the percentage change between censuses were determined by regression of the birth or death rate on the percentage change. Separate regressions were carried out on each of the 64 quadrats using the 21 census dates as samples. There was a significant positive correlation between percent change and birth rate in every test

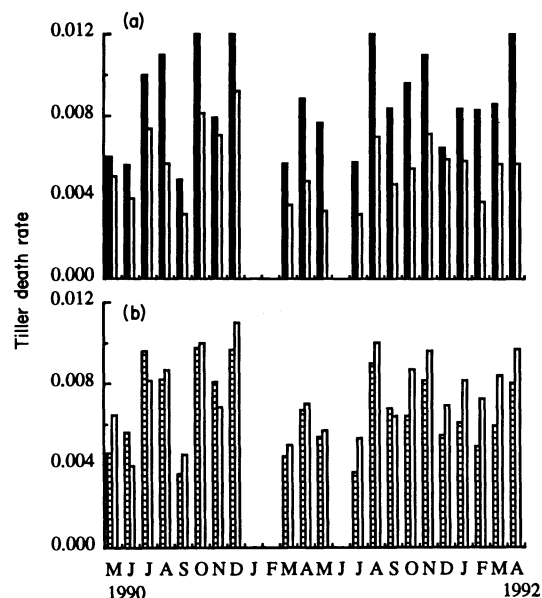


Fig. 5 The death rate of tillers (tillers tiller⁻¹ day⁻¹) from May 1990 to April 1992 under different treatments. (a) Each species pooled over the grazing treatments: ■, *Agrostis stolonifera*; □, *Lolium perenne*. (b) The effects of winter grazing pooled over the two species: ▨, non-winter-grazed; □, winter-grazed.

and a significant negative correlation with death rate in all but seven tests. However, in all 64 quadrats, a better fit to the percentage change data was given by birth rate (mean $r^2 = 0.72$) than the death rate (mean $r^2 = 0.37$). The reason for this lies in the fact that in each quadrat the coefficient of variation of the birth rate (mean over 64 quadrats = 99.2%) was greater

than that of the death rate (mean = 68.2%) as tested by a paired *t*-test using quadrats as samples ($t = 9.90$, $P < 0.001$). The variations in birth and death rates over time were rarely correlated with each other. Using the 21 census dates as samples, product-moment correlations of birth rates with death rates in each of the 64 quadrats were significantly negative to the 5% level in only five tests and to the 1% level in only one test.

Mean birth and death rates over the whole census period were significantly higher in the summer hard-grazed paddocks (0.0080 and 0.0075 tillers tiller⁻¹ day⁻¹, respectively) than in the summer-light-grazed paddocks (0.0071 and 0.0067 tillers tiller⁻¹ day⁻¹, respectively). However, there was no census–summer-grazing interaction and there was no summer grazing effect on percentage change in tillers.

DENSITY EFFECTS

The addition of the tiller density in the previous census as a covariate to the ANOVAS of the percentage change in tiller density, birth rate and death rate had little effect on the outcome of the analyses of grazing, species and census effects. No significant effects were lost and the summer grazing effect on the death rate became significant. Density only had significant effects on these three variables in the third stratum of the split-plot ANOVAS (Table 2). The correlations were negative for percentage change (coefficient = -0.325) and birth rate (-5.71×10^{-5}) and positive for the death rate (3.92×10^{-5}). Separate analyses of the two species showed no species differences in the coefficients of density effects on percentage change (coefficient ± 1 SE: *Agrostis*, -0.332 ± 0.061 ; *Lolium*, -0.372 ± 0.056), birth rate (*Agrostis*, $-5.9 \pm 1.4 \times 10^{-5}$; *Lolium*, $-5.3 \pm 1.2 \times 10^{-5}$) or death rate (*Agrostis*, $4.1 \pm 0.8 \times 10^{-5}$; *Lolium*, $4.4 \pm 0.9 \times 10^{-5}$).

SEEDLINGS

Very few seedlings appeared in the quadrats over the censusing period; less than 200 compared with the nearly 20 000 clonal tillers. *Lolium* produced 191 seedlings and *Agrostis* produced only 8. There were no grazing effects on seedling densities of either species. No seedling lived longer than 12 months and all died before the end of the experiment. No seed-derived tillers produced clonal tillers or flowered.

FLOWERING

Tillers flowered from May to August with the peak in June. Very few tillers of both species flowered in 1990 or 1991. In 1990 only 1.9% of *Agrostis* tillers flowered over the whole experiment and in 1991 none flowered. *Lolium* had a higher rate with 4.4% in 1990 but also showed a decreased rate in 1991 with 3.3% flowering. There were too few *Agrostis* data for ANOVA with

flowering occurring in only eight paddocks. ANOVA of the *Lolium* data showed that winter and spring grazing and increased grazing in summer all decreased flowering in 1990 but that there were no grazing effects in 1991 (Table 3).

Discussion

This study has indicated a number of factors affecting the tiller dynamics of *Lolium perenne* and *Agrostis stolonifera*, with some species differences in the response to these factors. These effects fall into four categories: within-year cyclical changes due to seasonal variation in the weather; the effects of between-year changes in the weather; grazing effects; and density-dependent population regulation.

SEASONAL DYNAMICS

Both species showed seasonal dynamics with tiller densities peaking in late summer and showing troughs in spring (Fig. 1a). Most studies of northern temperate clonal plant populations have shown this seasonal pattern (e.g. Eriksson 1986; Solbrig *et al.* 1980; Lovett Doust 1981; Thorhallsdottir 1983). However, a majority of these studies have shown summer peaks in both birth and death rates of ramets (but see Putwain *et al.* 1968); although these peaks are slightly asynchronous, producing summer peak in densities. In this study the seasonal changes in tiller densities of both species were caused by seasonal fluctuations in the birth rates (Fig. 4a). The between-census fluctuations in the death rates over the two years were not related to the seasons (Fig. 5a) and were less than those of birth rates, but they were consistent across treatments and between species (Fig. 5, Table 2). This indicates that some factor(s) caused these fluctuations, perhaps an interaction of seasonal and year-to-year changes in the weather.

Some workers have found that the initiation of flowering can cause a seasonal change in dynamics. Flowering may decrease birth rates and increase death rates (Langer *et al.* 1964; Bishop *et al.* 1978; Carlsson & Callaghan 1990a,b). Although Colvill & Marshall (1984) found this occurring in a population of *Lolium perenne*, neither species in our study showed seasonal changes in dynamics connected with flowering. This difference between the two studies is probably explained by the fact that Colvill & Marshall's (1984) population was not grazed and 25% of tillers flowered, whereas flowering was rare in our study.

YEAR-TO-YEAR CHANGES IN DYNAMICS

Apart from seasonal changes in abundance, ramet populations can be quite stable from year-to-year (e.g. Solbrig *et al.* 1980). However, year-to-year environmental changes may cause changes in ramet dynamics. For instance, year-to-year variation in the weather

Table 3 The main effects of grazing treatments on the percentage of *Lolium perenne* tillers in flowering 1990 and 1991

Grazing season	Winter			Spring			Summer		
Grazing intensity	+	−	<i>F</i> _{1,7}	+	−	<i>F</i> _{1,7}	3 cm	9 cm	<i>F</i> _{1,7}
1990	2.70	8.68	28.05**	3.14	8.24	20.36**	3.59	7.79	13.82**
1991	2.03	3.49	1.56	2.67	2.86	0.03	2.81	2.72	0.01

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ (F -values from ANOVA).

can have large effects on dynamics (Fowler 1986; Eriksson 1988; Jonsdottir 1991). There were indications in this study that the summer drought of 1990 depressed the birth rates of both species in June, July and August (Fig. 4a). This caused negative population changes in summer 1990, contrasting with the increases in summer 1991 (Fig. 3a).

GRAZING EFFECTS ON DYNAMICS

Transitory environmental changes may have only short term effects on dynamics. Our populations recovered rapidly from the drought (Fig. 1). More consistent environmental changes, such as the grazing treatments, may have more long term effects. The tiller densities of both species were decreased by winter grazing. This effect was first detected in September 1990 and continued throughout the subsequent censuses (Fig. 1b,c). However, the effects of long-term environmental changes may be complex, affecting only certain aspects of the ramet dynamics and only at discrete periods in the seasonal cycle (e.g. Noble *et al.* 1979; Barkham 1980; Carlsson & Callaghan 1990b). Butler & Briske (1988) found that grazing of the tussock grass *Schizachyrium scoparium* extended the seasonal peak in birth rate and brought forward the seasonal peak in death rate. In our study the winter grazing treatment affected the birth rate of both species by causing an earlier peak in winter-grazed populations (April–May) than in non winter-grazed populations (July–August) (Fig. 4b). However, the increased death rate under winter grazing was found in almost every census (Fig. 5b). The winter-grazing treatment effects on the birth rate brought about more positive changes in tiller densities in the non winter-grazed populations at particular censuses which tended to be between midsummer and autumn (Fig. 3b–d).

The mechanisms by which winter grazing affected the birth and death rates are unclear. The effects on the birth rate occurred only outside of the winter season and the effects on the death rate continued throughout the year. The effects of the summer grazing treatments – harder summer grazing increasing birth and death rates throughout the year (Table 2) – are also hard to explain. Direct effects of grazing obviously cannot explain effects occurring months after the treatment has ceased. Possible mechanisms may involve the carryover of environmental effects on

individual tillers (e.g. Bullock *et al.* 1993) or treatment effects on the age structure (e.g. Bishop *et al.* 1978; Noble *et al.* 1979) or size structure (e.g. Olsen & Richards 1988) of the tiller population. The grazing treatment effects on age-specific mortality and tillering rates will be investigated in another paper (Bullock *et al.*, unpublished).

DENSITY EFFECTS

The analyses indicated that tiller birth and death rates were both density-dependent (Table 2). It should be pointed out that although the correlations between density in the previous census and the birth or death rates might be labelled spurious because they share a common variable (i.e. density in the previous census), this is not a valid criticism because the analysis was carried out precisely to test for relationships between these variables (see Prairie & Bird 1989 for a fuller discussion of 'spurious correlations'). The density effects occurred only on the lowest stratum of the split-plot ANOVA (Table 2). This indicates, as would be expected, that density effects were present at the local, quadrat scale where they were detectable once effects of grazing treatments, species and replicates had been factored out. The seasonal and year-to-year changes in dynamics also had to be factored out in order to detect density-dependence. Planting experiments have sometimes found density-dependent tiller birth rates (Kays & Harper 1974; Hartnett & Bazzaz 1985; Lapham & Drennan 1987). However, the detection of density-dependence in unmanipulated field situations is more difficult. The interpretation that the seasonal peak in death rate that sometimes follows the peak in birth rate (Langer *et al.* 1964; Lovett Doust 1981; Navas & Garnier 1990) is a density response, is equivocal due to conflation with seasonal variation. Analysis of the factors affecting dynamics should therefore be structured to isolate the effects. Our study indicated that the ramet populations of *Lolium* and *Agrostis* were regulated by density-dependent birth and death rates but showed seasonal dynamics upon which were superimposed effects of grazing treatment and yearly variation in the weather. Other studies have shown that density-dependent regulation, seasonal variation, yearly variation and, in some cases, site differences, interact to affect ramet dynamics (Putwain *et al.* 1968; Weir 1985; Jonsdottir 1991).

BIRTH AND DEATH IN THE CONTROL OF
TILLER POPULATIONS

The tiller population densities were controlled by both the birth and death of tillers. Both processes were density-dependent and were affected by the grazing treatments, causing grazing effects on population sizes. However, there were strong indications that changes in population sizes in response to seasonal and year-to-year variation in the weather and the grazing treatments were caused more by changes in the birth rates than in the death rates. The effects of seasonal and year-to-year changes in the weather on tiller density were more attributable to their effects on birth rates rather than their effects on death rates (Figs 3a, 4a and 5a) because birth rates were more susceptible to variations in the weather and were therefore, more variable than death rates. Winter grazing affected both the birth and death rates but the grazing effects on population densities, which occurred at discrete time events (Fig. 3b), were attributable to large changes in the birth rates at these times (Figs 3c,d and 4c,d). This contrast in the responses of birth and death rates to the environment has not been found in other studies of ramet dynamics, although it has never been explicitly tested. It is probable that the control of the populations by variation in birth rates rather than death rates arises through the clonal nature of tiller production. Thus, tiller bud initiation is directly affected by the environmental conditions (e.g. Casal, Sanchez & Deregibus 1986) and increases in conditions favourable to survival. Therefore, the death of young tillers through birth into unfavourable conditions is low and population changes in response to the environment occur through changes in the birth rate.

SPECIES DIFFERENCES AND COMMUNITY
CHANGE

We found differences in the tiller turnover rates of the two species. *Agrostis* had a more rapid turnover of tillers than *Lolium* between most censuses and in all treatments (Figs 4a and 5a). This indicates intrinsic species differences in the control of tiller births (see above). As a result of this the *Agrostis* population densities were more variable than the *Lolium* densities. Although seedling establishment was of little importance in the dynamics of both species, the higher flowering rate of *Lolium* indicated a greater investment in sexual reproduction in this species. The higher seedling densities of *Lolium* supports this conclusion. Despite these differences, the two species showed similar seasonal and yearly variations in their dynamics (Figs 3a, 4a and 5a) and very similar responses to the grazing treatments (Table 2). These similarities occurred despite the effects of all the grazing treatments on species composition (Bullock *et al.* 1994). The only major species difference was in the responses

to the winter grazing treatment, which was however, only a quantitative difference. The species difference in the winter grazing effect on tiller densities arose through differences in the responses of the birth rates to winter grazing at only two censuses (Fig. 4c,d). Without understanding the mechanisms behind the responses of the two species to the grazing treatments (see above) it is difficult to explain the species differences and similarities in these responses. Jonsdottir (1991) showed differences among three grass species in the effects of several climatic variables on their tiller dynamics. Weir (1985) found differences between two grass species in the variation in their tiller dynamics between two sites. Neither author could explain these differences.

This study has provided an understanding of the rate and direction of community change under the grazing treatments. The two dominant species exhibited rapid tiller turnover with densities fluctuating seasonally but being regulated by density-dependent birth and death rates. Neither spring grazing nor interaction effects of the grazing treatments affected the tiller dynamics, and although there were effects of summer grazing treatment on tiller turnover rates, there were no effects on tiller densities. These results indicate that both species are able to maintain their population densities under different grazing treatments by having a plastic growth form. Surveys of the experiment have shown only small effects of the grazing treatments on the frequencies of the dominant species (Bullock *et al.* 1994). The fact that only the winter grazing treatment affected the densities of *Lolium* and *Agrostis* indicates that grazing in the winter is the treatment likely to bring about the most rapid change in species composition. Indeed, the surveys carried out by Bullock *et al.* (1994) showed that grazing in the winter had the most positive effect of all the grazing treatments on species number of the rare dicots and increased the abundances of more dicot species than did any other treatment.

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