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Plant demographic responses to environmental variation: distinguishing between effects on age structure and effects on age-specific vital rates

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Summary

1 The vital rates (e.g. fecundity, growth or mortality) of a plant population can each be expressed as the scalar product of the vectors \mathbf{n}_t , representing the age structure, and \mathbf{m}_t , representing the age-specific values of the vital rate. We hypothesize that environmental change can affect a vital rate of a plant population through one of two mechanisms: by changing the population age structure (hypothesis 1), or by altering the age-dependent vital rates (hypothesis 2).

2 We determined which of these hypotheses best explained the effects of different grazing treatments, applied in a field experiment, on the population tiller production of two pasture grasses, *Agrostis stolonifera* and *Lolium perenne*.

3 Monthly censuses of mean *per capita* tiller production were carried out for two years and grazing effects were detected in a number of censuses.

4 Tiller production by individual tillers was age-dependent and increased linearly with tiller age.

5 Grazing treatments significantly changed both the age structures (\mathbf{n}_t) of the tiller populations in most censuses and the regression of tiller production on age (\mathbf{m}_t) in a number of censuses.

6 Treatment effects on population tiller production predicted according to hypothesis 1 were calculated using measured values for \mathbf{n}_t specific to each grazing treatment and the mean values for \mathbf{m}_t over all treatments. Conversely, effects predicted according to hypothesis 2 were calculated using mean values for \mathbf{n}_t and values for \mathbf{m}_t specific to each grazing treatment.

7 The grazing effects on tiller production predicted by hypothesis 2 fitted the field data significantly for both species in all grazing treatments whereas hypothesis 1 never gave a significant fit. Therefore, grazing effects on population tiller production arose solely through changes in the age-specific values for tillering and never through effects on the population age structures.

8 We discuss the reasons for these results and consider the mechanisms of the responses to grazing. We also assess the use of these hypotheses in determining the ecological processes governing plant demographic change.

Keywords: *Agrostis stolonifera*, clonal plants, grazing, *Lolium perenne*, tiller production

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Introduction

A population's age structure is simultaneously the outcome of past demographic events and an indicator

of its demographic future. Present age structure reflects previous temporal variation in recruitment and mortality and, because vital rates in many populations are age-dependent, future age structure can be projected from present structure (see Caswell 1989). In plant populations, age structures typically reflect the past impact of factors such as grazing (e.g. Crisp & Lange 1976), fire (e.g. Frissell 1973) and forest

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canopy opening (e.g. Kanzaki 1984). Although the majority of studies of plant population age structure have been confined to woody plants in which the determination of age is relatively easy, perennial herbs have age structures that are influenced by a variety of environmental factors (e.g. Noble, Bell & Harper 1979; Gatsuk *et al.* 1980; Silva *et al.* 1991; O'Connor 1993).

If vital rates are age-dependent, it is possible to distinguish two fundamentally different ways in which environmental factors may perturb the demography of a population; 1. by a simple change in age structure or 2. by directly altering the relationship between vital rates and age. To illustrate this distinction in terms of the vital rate fecundity (this could be applied equally to other vital rates, e.g. mortality), let \mathbf{n}_t be a column vector representing the age structure of a population (i.e. a list of the numbers of individuals in each age class at time t) and let a column vector \mathbf{m}_t be the fecundity schedule (i.e. a list of the average numbers offspring born to plants in each age class). Then, total recruitment, R_t , over the time period t (e.g. a year) is the scalar product of age structure and fecundity schedule:

$$R_t = \langle \mathbf{n}_t, \mathbf{m}_t \rangle \quad (1)$$

Recruitment can be influenced by altering age structure \mathbf{n}_t (e.g. through differential mortality rates between age classes), or fecundity schedule \mathbf{m}_t (i.e. altering age-specific fecundity values), or both. The two kinds of perturbation are fundamentally different because a change to a population's age structure will in time be corrected if age-specific vital rates are stationary, but a change to the age-specific relationship of vital rates themselves will alter the equilibrium age distribution (Caswell 1989). The influence of the first kind of effect may be short-lived, while the influence of the second will reverberate down the generations. Despite the importance of this distinction, it appears to have received little attention hitherto.

Obviously, both age structure and age-dependent vital rates may be affected by environmental change and both mechanisms may act concurrently. Therefore, it is not sufficient to know whether or not there are environmental effects on \mathbf{n}_t and/or \mathbf{m}_t , but also to understand the relative importance of these two fundamentally different processes. Such an analysis will allow us to elucidate the mechanisms of the population response to environmental change and to understand and predict the future dynamic consequences of these changes.

In this paper we present a method for distinguishing between perturbations to population vital rates that act through changes to age structure and those that act through changes in the age-specific relationship of vital rates, and we apply the method to an experimental field study of the effects of grazing on the tiller demography of two grasses (Bullock *et al.* 1994a). In this case the vital rate we analyse is tiller

production, but the method is equally applicable to other vital rates. The design of the experiment permitted us to apply contrasting intensities of sheep grazing in a part of the year and then to follow the subsequent effects of these treatments on tiller demography. We found that the effects of seasonal grazing on tiller production were delayed and lasted many months after the cessation of treatments. Two alternative hypotheses to explain the delayed and long-lasting effects are tested here; 1. The effect of grazing on tiller age structure (\mathbf{n}_t) was the dominant mechanism causing changes in population tiller production. 2. The effect of grazing on age-specific tiller production (\mathbf{m}_t) was the dominant mechanism. Because grazing treatments were applied and then removed (a 'pulse' experiment, *sensu* Bender *et al.* 1984) we expected to find support for hypothesis 1 rather than hypothesis 2.

Testing these two hypotheses requires a detailed knowledge of the age-dependence of vital rates. Although this relationship has been well studied for non-clonal plants (Werner & Caswell 1977; Leverich & Levin 1979; Hara 1988), there has been little work on age dependence in clonal ramets (but see Eriksson 1988; Carlsson & Callaghan 1991). Therefore, a second objective of this paper is a comprehensive evaluation of the age dependence of clonal growth in grass tillers.

Materials and methods

STUDY SYSTEM

Agrostis stolonifera and *Lolium perenne* are both fast growing grasses with low, spreading growth forms. They are dominant species in the fertile pastures of lowland Britain. The grazing experiment was set up at Little Wittenham Nature Reserve in Oxfordshire, southern England (15°37'N, 1°10'W) in 1986 (Treweek 1990). The site was regularly fertilized until 1984 and the vegetation is species-poor and dominated by fast-growing agricultural grasses (Bullock *et al.* 1994b). Average annual rainfall is 605 mm evenly distributed throughout the year. Temperatures peak in July (mean maximum 21.6 °C, minimum 11.6 °C) and are lowest in January (mean maximum 6.0 °C, minimum 1.0 °C).

Grazing treatments were applied to 0.25 ha plots every year 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 these levels were, ungrazed (designated –) or grazed (designated +) by two sheep per plot. In summer these levels were, light-grazed (sward height maintained at 9 cm) or hard-grazed (3 cm sward height). These summer levels were also designated – and +, respectively. The two levels for each grazing season were factorially combined to give a 2 × 2 × 2 struc-

ture in two randomized blocks assigned over 16 (2 × 8) plots.

TILLER DEMOGRAPHY

Our basic study of tiller demography is fully described by Bullock *et al.* (1994a), and only essential details will be given here. Tiller populations were followed in four 10-cm × 10-cm quadrats in each of the 16 plots. *Lolium perenne* was censused in two of the quadrats and *Agrostis stolonifera* in the remaining two. The populations were first censused in April 1990, when all tillers of the target species rooted within the quadrat were counted and marked at the base with a spot of acrylic poster paint. Only tillers at or beyond the first leaf stage were marked. Censuses were carried out monthly until April 1992 with three censuses missed due to bad weather. 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. The cohort of the parent tiller of each new tiller was noted. Most tillers were of clonal origin and an average of 95% of clonal tillers of both species derived from parent tillers within the quadrat. In the first census there was an average of 55 tillers of the target species in each quadrat.

ANALYSIS

Agrostis and *Lolium* were analysed separately and only data on the clonal tillers were used. We assumed that the death of tillers between each census occurred simultaneously and midway between censuses. Tiller-ing also occurred midway between censuses but instantaneously after tiller death. Therefore, no tillers which died between censuses tillered as well. This latter assumption was supported by our field observations. We also assumed that no new tillers died before they could be censused, and that no new tillers themselves tillered before their first census. This assumption was occasionally violated but too rarely to have consequences for this analysis.

POPULATION TILLER PRODUCTION

The mean daily *per capita* tiller production, R_t , of the tiller population in each quadrat was calculated for a census at time t as

$$R_t = (n_N/n_O)(1/L), \quad (2)$$

where n_N is the number of new tillers at time t and n_O the number of old tillers at time t and L the length of census interval (days). New tillers were those produced between censuses $t-1$ and t , old tillers were those surviving between these two censuses, and the census interval was the period from the midpoint between the censuses $t-2$ and $t-1$ until the midpoint between the censuses $t-1$ and t . (The 'tiller birth rate' used by Bullock *et al.* (1994a) was calculated slightly

differently, using the number of tillers at the previous census as the denominator.) For each of the 22 censuses, values of R_t were calculated for every quadrat and a species value was obtained for each plot by averaging over the two appropriate quadrats. The significance of grazing treatment effects on R_t were determined by three-way ANOVAs (two levels of grazing in each of three grazing seasons) for both species in each of the 22 censuses.

The values of R_t specific to each grazing level in winter, spring and summer were calculated by taking averages across the appropriate sets of plots. These values were designated R_t^{g+} and R_t^{g-} for + and – levels of grazing, respectively. For each grazing season we determined the values of R_t^{g+} and R_t^{g-} of both species in each of the 22 censuses.

METHODOLOGY FOR HYPOTHESIS TESTING

We tested the two hypotheses by comparing the ratios of R_t^{g+} to R_t^{g-} predicted by each hypothesis with the ratios observed in the field. Using eqn 1, the tiller production of a population (R_t) is the scalar product of the age structure (\mathbf{n}_t) and the age-specific tiller production (\mathbf{m}_t) of that population. To determine the relative contributions of \mathbf{n}_t and \mathbf{m}_t to interpopulation variation in R_t our basic procedure was to estimate two sets of values of R_t for each population, first allowing interpopulation variation in \mathbf{n}_t alone and secondly using only interpopulation variation in \mathbf{m}_t . Thus, the variation in R_t between populations was partitioned between variation in age structure and variation in age-specific tillering.

Under hypothesis 1, grazing effects on R_t should be the result of changes to \mathbf{n}_t alone, and therefore the tiller production in a + grazing level at census t should be

$$R_t^{g+} \propto \langle \mathbf{n}_t^{g+}, \mathbf{m}_t' \rangle, \quad (3)$$

where \mathbf{n}_t^{g+} is the proportional age structure in the relevant grazing treatment and \mathbf{m}_t is the vector of age-specific tiller production averaged over all treatments; the right hand side of the equation is their scalar product. The corresponding equation for a – grazing treatment is

$$R_t^{g-} \propto \langle \mathbf{n}_t^{g-}, \mathbf{m}_t' \rangle. \quad (4)$$

If hypothesis 1 is correct then the following relationship should hold

$$R_t^{g+}/R_t^{g-} \propto \langle \mathbf{n}_t^{g+}, \mathbf{m}_t' \rangle / \langle \mathbf{n}_t^{g-}, \mathbf{m}_t' \rangle. \quad (5)$$

Under hypothesis 2, grazing effects on R_t should be the result of changes in \mathbf{m}_t alone and therefore, using an argument symmetrical with that already employed, the tiller production in a + grazing level at census t should be

$$R_t^{g+} \propto \langle \mathbf{n}_t, \mathbf{m}_t^{g+} \rangle, \quad (6)$$

where \mathbf{n}_t is the proportional age structure averaged over all treatments and \mathbf{m}_t^{g+} is the vector of age-specific tiller production in the relevant grazing treatment. If hypothesis 2 is correct then the following relationship should hold

$$R_t^{g+}/R_t^{g-} \propto \langle \mathbf{n}_t, \mathbf{m}_t^{g+} \rangle / \langle \mathbf{n}_t, \mathbf{m}_t^{g-} \rangle. \quad (7)$$

AGE STRUCTURE

For each species we determined the average tiller population age structure (\mathbf{n}_t) at each census from August 1990 to April 1992 by combining the data from all plots. The age structures for both grazing levels in each grazing season (\mathbf{n}_t^{g+} and \mathbf{n}_t^{g-}) were calculated by combining data over the eight plots receiving a grazing level (4 treatments \times 2 blocks). *G*-tests were used at each census to determine the significance of the difference between \mathbf{n}_t^{g+} and \mathbf{n}_t^{g-} for each of the three grazing seasons. If a cohort in either grazing level contained less than five tillers it was merged with the previous cohort (see Sokal & Rohlf 1981; p. 709). The tiller group from the April 1990 census and the new tiller cohort were excluded from these analyses (see below).

AGE-SPECIFIC TILLER PRODUCTION

For each surviving cohort in a census we calculated: (i) the tiller age (x) at the time of tillering, and (ii) the per capita tiller production (m_x).

$$m_x = \frac{\text{no. of tillers produced by cohort } x \text{ at census } t}{\text{no. of tillers of cohort } x \text{ at census } t}. \quad (8)$$

The ages of the tillers present in the first census (April 1990) could not be known so this group did not constitute a cohort and was excluded from this analysis, although it did produce tillers. The new tiller cohort in each census could not, by definition, produce tillers and was therefore excluded from the analysis. Two values of m_x , one using the merged data from all plots on block 1 and the second for block 2, were calculated for every cohort at each census. We determined the relationship between m_x and age by regressing m_x on x for each census from August 1990 to April 1992 (18 censuses). Three cohorts were tillering in August 1990, giving $n = 6$ (3 cohorts \times 2 blocks), and the sample size was larger in later censuses. The data were normally distributed. The regression equations were used to provide the values for the vectors of age-specific tiller production (\mathbf{m}_t) averaged over all treatments required to test hypothesis 1.

We then determined the effects of grazing treatments on the relationship between x and m_x for the \mathbf{m}_t^{g+} and \mathbf{m}_t^{g-} vectors needed to test hypothesis 2. Values of m_x were calculated for + and – grazing levels in each of the three grazing seasons for each

block by merging the data from the appropriate plots. Differences in the regression lines between the two levels of winter grazing, the levels of spring grazing and the levels of summer grazing were tested for by ANOVAS (Genstat 5 Committee 1989). Where grazing significantly affected the regression the equation specific to the appropriate grazing treatment was used to calculate \mathbf{m}_t^{g+} or \mathbf{m}_t^{g-} . Otherwise, the \mathbf{m}_t vector using values averaged over all treatments was used.

TESTING THE HYPOTHESES

These derived data were used to calculate the expected ratios of R_t^{g+} to R_t^{g-} for hypothesis 1 (using eqn 5) and hypothesis 2 (using eqn 7) for each seasonal grazing treatment in every census. These were calculated separately for *Agrostis* and for *Lolium*. For each hypothesis and each species we determined the correlations of these expected ratios with the observed ratios of tiller production between + and – grazing in winter by Spearman rank correlation, using each census as a sample. Correlations were also estimated for both spring and summer grazing level effects.

Although the tillers present in the first census in April 1990 (designated 'AG') were excluded from the calculations of the expected R_t ratios because their ages were unknown, they contributed a great deal to the population tiller production. To assess the consequences of excluding this tiller group from the analyses we calculated a second set of expected ratios for each census and determined their correlations to the observed data. The second set of ratios for hypothesis 1 were calculated by taking the average number of AG tillers across all treatments and including this as an extra element in \mathbf{n}_t . The average tiller production of this group was then calculated for each grazing level and added to the \mathbf{m}_t^{g+} and \mathbf{m}_t^{g-} vectors. Elements for the AG tillers were added to the \mathbf{m}_t , \mathbf{n}_t^{g+} and \mathbf{n}_t^{g-} vectors to calculate the second set of ratios for hypothesis 2.

Results

POPULATION PER CAPITA TILLER PRODUCTION, R_t

Although tiller production was calculated slightly differently, the values showed very similar grazing effects and temporal changes to the 'tiller birth rate' found for the same data by Bullock *et al.* (1994a), and that study should be referred to for a fuller discussion of these responses. There were very few interaction effects among grazing seasons and we shall discuss the responses to the main grazing treatments only. The number of censuses which showed significant responses of R_t to grazing level were many more than expected by chance for winter, for spring and for summer grazing in both species (Fig. 1). The direction of these effects varied among censuses and the tem-

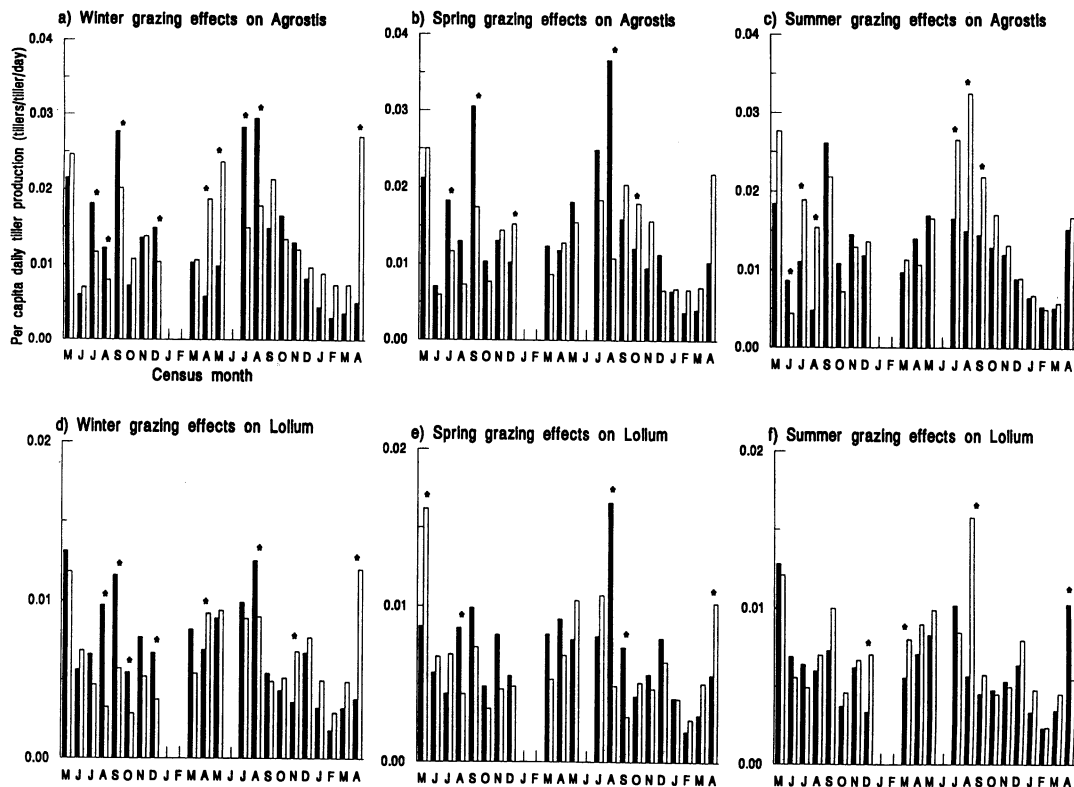


Fig. 1 Responses of the population *per capita* tiller production (R_t) per day of each species to grazing level in each season from May 1990 to April 1992. Censuses were missed in January 1991, February 1991 and June 1991. (a) Winter grazing effects on *Agrostis stolonifera*. (b) Spring grazing effects on *Agrostis*. (c) Summer grazing effects on *Agrostis*. (d) Winter grazing effects on *Lolium perenne*. (e) Spring grazing effects on *Lolium*. (f) Summer grazing effects on *Lolium*. ■ – grazing level; □ + grazing level. * indicates a significant effect of the relevant grazing treatment was found in that census.

poral pattern of effects differed between the species, except for the similar pattern of winter grazing effects in *Agrostis* and *Lolium* (Fig. 1a,d).

Most of these responses to grazing occurred at censuses outside of the relevant grazing season. The proportions of the censuses showing significant grazing effects on R_t that fell outside the grazing season are as follows. Winter grazing effects on *Agrostis*, 6/9; and on *Lolium*, 5/8; spring grazing effects on *Agrostis*, 5/5; and on *Lolium*, 3/5; summer grazing effects on *Agrostis*, 1/6; and on *Lolium*, 3/4. These effects were all more common than expected by chance.

AGE-SPECIFIC TILLER PRODUCTION

The regression of m_x on cohort age for *Agrostis* was significant at $P < 0.05$ in 13 of the 18 censuses and was weakly significant at $P < 0.1$ in two censuses (Fig. 2). For *Lolium*, 12 regressions were significant at $P < 0.05$ and two at $P < 0.1$ (Table 1). Where it was significant, the relationship was always positive and there were no indications that a nonlinear regression model would have had a consistently better fit to the data. The m_x values of the April 1990 tiller group are included in Fig. 2 for *Agrostis* and these values were generally higher than or similar to those of the oldest cohort. The *Lolium* data showed the same trend (data are not shown).

ANOVA of grazing effects on the regression line showed the significance of grazing level as a main effect ('intercept' effects) and of the interaction effect of age \times grazing level ('slope' effects). The former indicated a consistent and similar effect of grazing level on the m_x of all cohorts, but the latter indicated that the effect of grazing on m_x changed with cohort age. Intercept or slope differences between winter grazing levels for *Agrostis* were found in August and September 1990, May, July and August 1991 and February and April 1992 (Fig. 3). We also found winter grazing effects on the population tiller production (R_t) in all but one of these censuses (Fig. 1a). *Lolium* showed winter grazing effects on the regression line in August, September and October 1990, August and November 1991 and March and April 1992 (Table 2). Again, these mirrored effects on the population tiller production in all but one census (Fig. 1d).

Although both intercept and slope effects of winter grazing were found (Fig. 3, Table 2), the effects were almost always due to all cohorts having higher values of m_x in one of the grazing levels; the more complex slope effects were caused by small responses to grazing at low ages, but an increased grazing effect in older cohorts (e.g. Fig. 3b). The only exception to this is seen in Fig. 3a.

The relationship between m_x and x in both species was also significantly affected by both spring and sum-

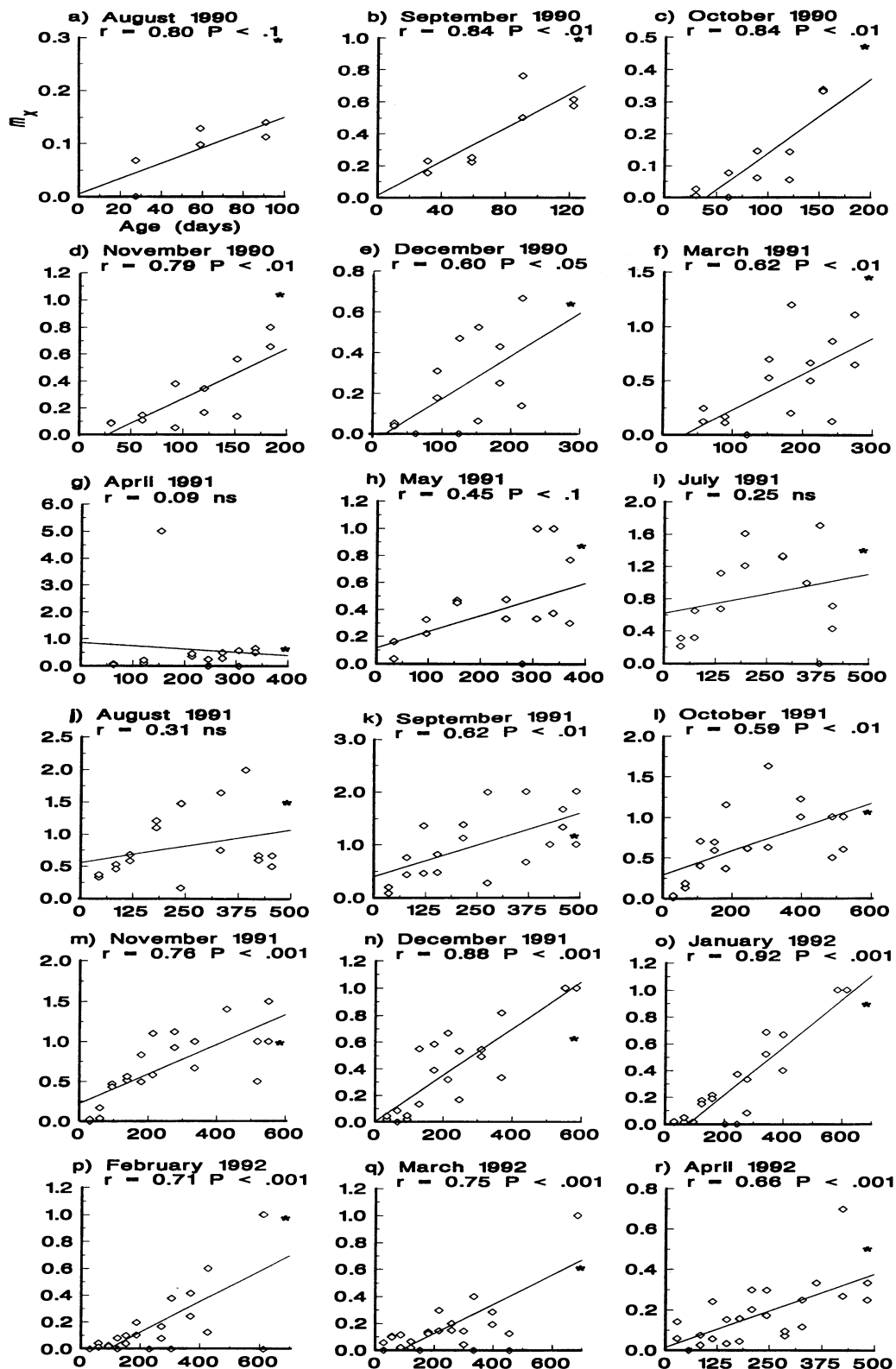


Fig. 2 Linear regressions of age-specific *per capita* tiller production (m_x) on cohort age in each census for *Agrostis*. The isolated symbol * is the m_x of the initial April 1990 tiller group, which was not included in the regressions.

Table 1 Results of linear regressions of age-specific *per capita* tiller production (m_x) on cohort age (days) in each census for *Lolium*. The fitted gradient, the intercept and the regression coefficient, r , and its significance are shown for each of the 18 censuses

Census month	Fitted gradient	Fitted intercept	r
August 1990	12×10^{-4}	6×10^{-3}	0.65
September 1990	15×10^{-4}	12×10^{-3}	0.90**
October 1990	5×10^{-4}	5×10^{-3}	0.66*
November 1990	4×10^{-4}	76×10^{-3}	0.24
December 1990	5×10^{-4}	15×10^{-3}	0.35
March 1991	16×10^{-4}	23×10^{-3}	0.47†
April 1991	10×10^{-4}	34×10^{-3}	0.36
May 1991	10×10^{-4}	31×10^{-3}	0.61*
July 1991	14×10^{-4}	178×10^{-3}	0.52*
August 1991	9×10^{-4}	192×10^{-3}	0.42†
September 1991	1×10^{-4}	5×10^{-3}	0.59**
October 1991	9×10^{-4}	46×10^{-3}	0.52*
November 1991	18×10^{-4}	130×10^{-3}	0.62**
December 1991	11×10^{-4}	15×10^{-3}	0.62**
January 1992	16×10^{-4}	139×10^{-3}	0.65**
February 1992	5×10^{-4}	30×10^{-3}	0.61**
March 1992	8×10^{-4}	2×10^{-3}	0.51**
April 1992	7×10^{-4}	26×10^{-3}	0.71***

† $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

ing effects on the population tiller production, R_t . For *Lolium*, there was a significant effect of spring grazing on the regression in four censuses and on the tiller production in four, and coincident effects on both the regression and the tiller production were found in three of these censuses. In the remaining analyses the corresponding figures were: spring grazing effects on *Agrostis*, 5, 4, 4; summer grazing on *Agrostis*, 4, 4, 3; and summer grazing on *Lolium*, 4, 4, 3.

AGE STRUCTURE

The G -tests on both species showed significant winter, spring and summer grazing level effects on the tiller age structure in most censuses. Of the 18 censuses there was no significant grazing effect in three censuses for summer grazing effects on *Agrostis*, in three censuses for winter grazing effects on *Lolium*, and in seven censuses for summer grazing effects on *Lolium*. There were significant grazing effects in all censuses for the winter and spring grazing effects on *Agrostis* and for spring grazing effects on *Lolium*. These analyses are too many to show, but Fig. 4 shows the grazing effects on the age structures in the final census. Both species showed skewed age distributions in all treatments and the median cohort age was generally higher in *Lolium* (148–208 days) than in *Agrostis* (148 days).

A TEST OF THE HYPOTHESES

There were no significant results in six tests (3 grazing seasons \times 2 species) of correlation between the observed ratio of R_t^{g+} to R_t^{g-} and the ratios estimated under hypothesis 1 (Table 3). The addition of tiller production by the April 1990 (AG) tiller group did not change this result, apart from a positive correlation in one test. In contrast, all six tests of correlation between the observed ratios and the ratios estimated under hypothesis 2 were significant. The second set of estimates of ratios for hypothesis 2, including tillering by the AG tiller group, showed no overall better or worse correlation than when this group was excluded. Thus, it was not necessary to include this group of tillers of unknown age in the test of the hypotheses.

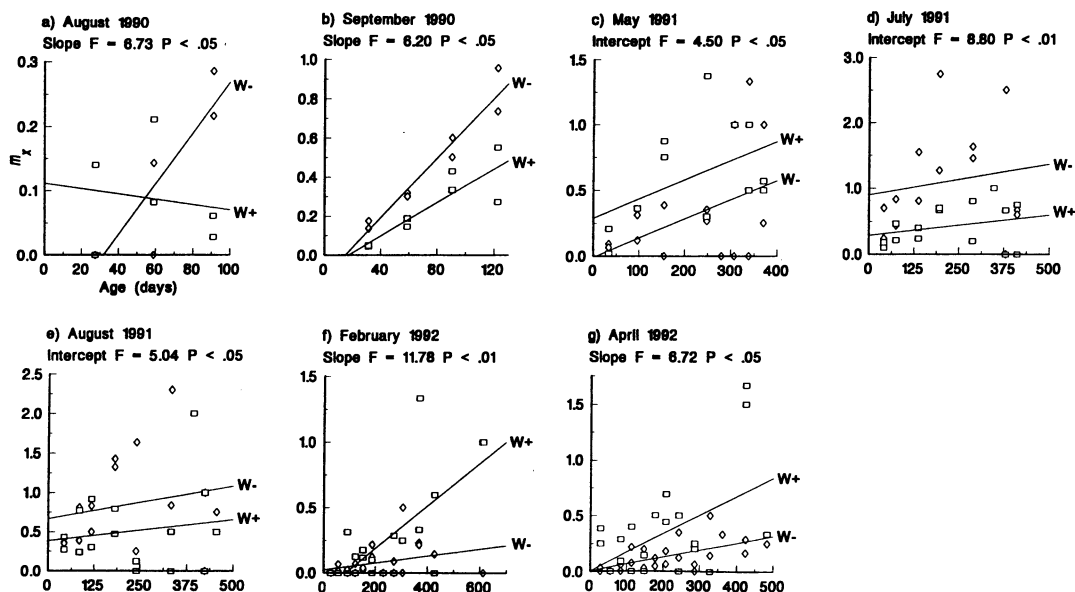


Fig. 3 Winter grazing effects on the regression of m_x on cohort age for *Agrostis*. We show only those censuses in which there was a significant effect of either grazing treatment ('intercept') or age \times grazing treatment ('slope'). \square grazed in winter (W+); \diamond not grazed in winter (W-).

Table 2 Results of ANOVAS of winter grazing effects on the regression of m_x on tiller age for *Lolium* (effects on *Agrostis* are illustrated in Fig. 3) and of ANOVAS of spring or summer grazing effects on this regression for both species, *Agrostis* and *Lolium*. This was carried out on each of the 18 censuses from August 1990 to April 1992 but we show only the censuses for which we found a significant difference in the regressions between the grazing levels. Grazing level could affect the regression as a main effect ('intercept' effects) or an effect of age \times grazing level ('slope' effects). These are indicated, respectively, by the superscripts i and s

Census	F
Winter grazing	
<i>Lolium</i>	
August 1990 ^s	6.7*
September 1990 ^s	6.2*
May 1991 ⁱ	4.5*
July 1991 ⁱ	8.8**
August 1991 ⁱ	5.1*
February 1992 ^s	11.3**
April 1992 ⁱ	6.7*
Spring grazing	
<i>Agrostis</i>	
August 1990 ⁱ	7.4*
September 1990 ⁱ	4.8*
December 1990 ⁱ	5.5*
August 1991 ^s	10.8**
October 1991 ^s	9.1**
<i>Lolium</i>	
May 1991 ⁱ	12.5**
August 1991 ⁱ	21.9***
September 1991 ⁱ	13.5***
April 1992 ⁱ	4.2*
Summer grazing	
<i>Agrostis</i>	
March 1991 ⁱ	4.8*
July 1991 ⁱ	5.8*
August 1991 ⁱ	5.3*
September 1991 ⁱ	4.9*
<i>Lolium</i>	
December 1990 ⁱ	6.3*
August 1991 ⁱ	4.5*
March 1992 ⁱ	4.9*
April 1992 ⁱ	6.0*

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

Discussion

AGE STRUCTURE HYPOTHESIS VS. AGE-SPECIFIC TILLERING HYPOTHESIS

Both mechanisms could have had a role in explaining the grazing effects on the population *per capita* tiller production. Indeed, there were winter, spring and summer grazing effects on both the population age structures (Fig. 4) and on the regressions of m_x on age (Fig. 3, Table 2). Our analysis aimed to determine which was the more important mechanism. The results showed that only the variation in age-specific tiller production explained the interpopulation variation in tiller production to a significant degree (Table 3). The good fit of hypothesis 2 is explained by the fact that significant grazing effects on the regressions of m_x on age occurred in generally the same censuses

as did effects on the population tiller production. Although the grazing treatments affected tiller age structures in most censuses, these effects were subtle (note that in the final census the medians of the tiller ages were similar in the two levels of winter, of spring and of summer grazing; Fig. 4). Because of this, the estimates of the ratios under hypothesis 1 varied little among the censuses [e.g. the coefficient of variation of the winter grazing ratios for *Agrostis* estimated under hypothesis 1 was 0.152, and was much less than those of the observed ratios (CV = 0.779) or of the ratios estimated under hypothesis 2 (CV = 0.597)].

The clear confirmation of hypothesis 2 and the equally clear falsification of hypothesis 1 were a surprise to us. We expected the reverse because the majority of significant winter, spring and summer grazing effects occurred at censuses outside of the relevant grazing seasons. The age structure reflects past temporal variation in recruitment and mortality and thus perturbations to the age structure caused by a grazing treatment might be apparent some months after the end of the grazing season. However, enduring effects on the vital rates of individual tillers are less easy to understand. Although there were long-term grazing effects on tiller density, these indirect effects on tiller production were not density-induced; the responses remained after we factored out density as a covariate (Bullock *et al.* 1994a). We may resolve the mechanism behind these responses through an understanding of the age-dependence of tiller production.

AGE-DEPENDENT TILLERING

We found a straightforward linear correlation between age and m_x in both species and at most censuses and the cases showing lack of fit were due to the scatter of the data rather than any nonlinearity of the relationship (Fig. 2). Another aspect of this relationship is that there was no evidence of an age threshold for tillering. The regressions of m_x on age had negative intercepts in only roughly half of the data sets and even in these cases the youngest cohort only rarely had a zero value of m_x .

These findings provide an insight into the demography of natural populations of clonal plants which is unique in its detail and simplicity. We can locate only three comparable studies which have, however, been on tundra species with very long-lived ramets. Fetcher & Shaver (1983) followed the tiller dynamics of the sedge *Eriophorum vaginatum* (maximum age 15 years) and their data show, apart from low m_x values for very young tillers, no correlations between tillering and age. Proliferation of apex modules (maximum age 21 years) of the club moss *Lycopodium annotinum* peaked at 8–10 years old (Svensson & Callaghan 1988) and *per capita* tiller production of the sedge *Carex bigelowii* (maximum age 6 years) peaked at 1–2 years old (Carlsson *et al.* 1990). Comparisons with these

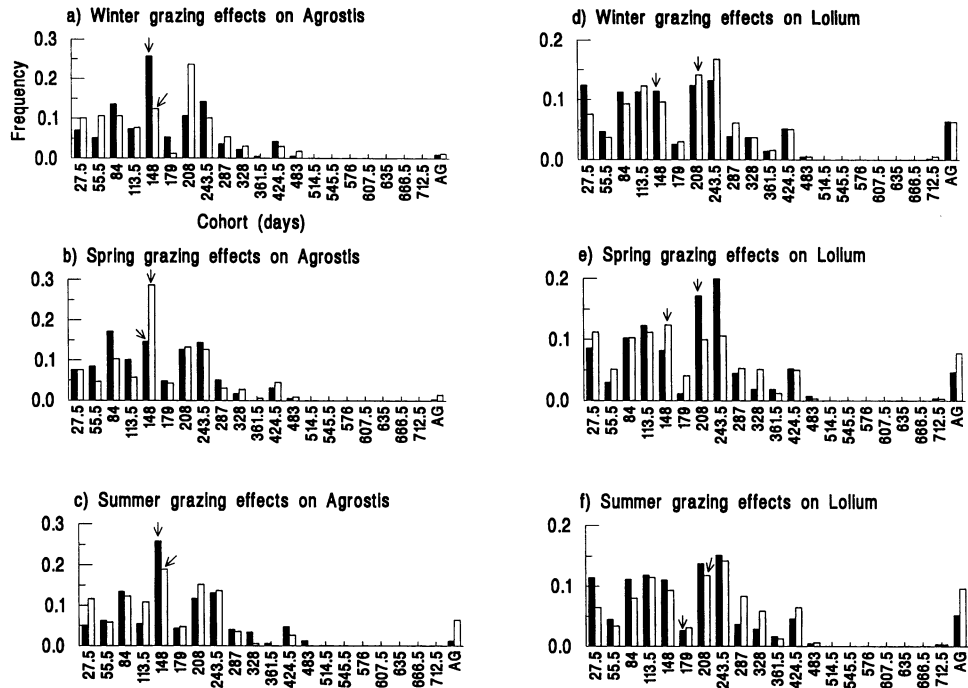


Fig. 4 The differences between the age structures in April 1992 of the populations in each grazing level for each grazing season. AG is the initial April 1990 tiller group which was given an age corresponding to the time since the first survey. The arrow indicates the median age group. ■ – grazing level. □ + grazing level. (a) Winter grazing effects on *Agrostis* $G = 46.7$, d.f. = 10, $P < 0.001$. (b) Spring grazing effects on *Agrostis* $G = 46.1$, d.f. = 10, $P < 0.001$. (c) Summer grazing effects on *Agrostis* $G = 38.6$, d.f. = 9, $P < 0.001$. (d) Winter grazing effects on *Lolium* $G = 23.7$, d.f. = 12, $P < 0.05$. (e) Spring grazing effects on *Lolium* $G = 61.3$, d.f. = 12, $P < 0.001$. (f) Summer grazing effects on *Lolium* $G = 27.0$, d.f. = 12, $P < 0.01$.

studies should be made tentatively because our system was very fertile and a majority of tillers lived for less than 12 months (Bullock unpublished data).

Some studies of ramet populations have shown size-dependent seed production (Eriksson 1988; Carlsson & Callaghan 1990) or ramet proliferation (Eriksson 1988; Mendez & Obeso 1993). The age and

size of ramets may be correlated (e.g. Callaghan 1976; McGraw 1989; Hanzawa & Kalisz 1993) and therefore our finding of greater m_x by older tillers may have been due to age-related increases in tiller size. The tillers were grazed and therefore, above-ground size of tillers (e.g. biomass or height) will have varied rapidly over time and certainly would not have been correlated with age. However, older tillers may have had greater below-ground size (e.g. root biomass) and this might have conferred competitive superiority and thus higher tiller production.

As an alternative to these size-related mechanisms, the age of a tiller may indicate its ontogenetic stage (see Gatsuk *et al.* 1980) and older tillers would have a greater number of tiller buds or a greater propensity for the initiation of tiller bud development. However, grasses have a higher level of organization than the tiller, that of the interconnected group of tillers. This group may be physiologically interdependent and therefore the tillers will not respond to the environment as individuals but rather the tiller group will act together (e.g. Welker *et al.* 1991; Williams & Briske 1991) as an 'integrated physiological unit' (IPU; Watson & Caspar 1984). Therefore, assuming that the *Lolium* and *Agrostis* populations consisted of groups of interconnected tillers of different ages, the age-specific tillering may have reflected an internally controlled pattern of resource allocation in each IPU. Thus, the older tillers constrained the tillering of the younger ones. Such apical dominance has been seen in a number of clonal plants (Jonsdottir & Callaghan

Table 3 Coefficients of Spearman rank correlations of the observed ratios of R_{t+}^+ to R_{t+}^- (*per capita* tiller production between the two grazing levels of a grazing season) with the ratios estimated according to hypothesis 1 (grazing effects on tiller age structure \mathbf{n}_t caused changes in population tiller production) or hypothesis 2 (grazing effects on age-specific tiller production structure \mathbf{m}_t caused these changes). Two sets of ratios were calculated under each hypothesis: one including tiller production by the April 1990 tiller group ('+ AG') and the other not ('- AG'). The data from 18 censuses (August 1990 – April 1992) were used as samples for each correlation

Species/ Grazing season	Hypothesis 1		Hypothesis 2	
	- AG	+ AG	- AG	+ AG
<i>Agrostis</i>				
Winter	0.073	0.088	0.579*	0.571*
Spring	0.214	0.474*	0.653**	0.709***
Summer	0.294	-0.001	0.488*	0.593**
<i>Lolium</i>				
Winter	-0.421	-0.168	0.858***	0.948***
Spring	-0.209	0.137	0.662**	0.893***
Summer	0.278	0.333	0.608**	0.591**

1988; Svensson & Callaghan 1988; Bullock *et al.* 1994c). In our study the very similar responses of the different cohorts to the grazing treatments (Fig. 3) suggests that the tillers were responding to the environment in groups rather than as individuals. In the simplest cases the grazing treatment changed the m_x values of all the cohorts to the same extent (e.g. Fig. 3c). Otherwise, the direction of the grazing effect on m_x was the same for all ages but the difference was greater in the older cohorts (e.g. Fig. 3b), indicating that the older tillers had a greater plasticity of tiller production.

If tiller groups were indeed responding in an ecologically integrated fashion to the environment then the long-term, out-of-season effects of the grazing treatments are less surprising. The plant formed by the IPU will live much longer than individual tillers. Therefore environmental effects on such traits as its concentrations of reserves, root biomass or tiller number may cause a continuing response after the perturbation has ceased and therefore affect its growth rate, measured by the tillering of its individual tillers. For example plants grazed in the winter may have had reduced vigour that continued to affect their ability to tiller throughout the year. This interpretation is speculative, but the analysis has served to refine our hypothesis of the mechanism of population response to environmental change and to pinpoint areas for further research.

ENVIRONMENTAL EFFECTS ON DEMOGRAPHY

The technique described in this paper can use the rich data from demographic studies to aid us in searching for the processes behind population change. Although hypothesis 2 turned out to be the successful hypothesis for both species in this instance, there is no reason to believe that this will be a general result. We carried out another demographic study in this grazing experiment, using a very different plant, the monocarpic perennial *Cirsium vulgare* (Bullock *et al.* 1994d). This study investigated size-specific, rather than age-specific, vital rates, but a general comparison is still valid. If we re-evaluate the *Cirsium* study in the light of this paper we can see that winter grazing effects on the fecundity of the populations were explained by hypothesis 1 rather than hypothesis 2; grazing changed the population size structure but had no effect on the size-dependent flowering probability. Therefore, the mechanisms of demographic response to environmental change may differ among species and indeed, may depend upon the environmental factor involved. As this study has shown, it would be unwise to predict how these factors will affect the validity of each hypothesis.

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