

Effects of density and weather on tiller dynamics in *Agrostis stolonifera*, *Festuca rubra* and *Poa irrigata*

G. Á. JÓNSDÓTTIR

Department of Botany, University of Stockholm, S-106 91 Stockholm, Sweden

SUMMARY

Tiller populations of three grass species, *Agrostis stolonifera*, *Festuca rubra* and *Poa irrigata* (= *Poa pratensis* ssp. *irrigata*), were studied for 5 years on a Baltic seashore meadow in Sweden. No significant relationships were found between the death rate of tillers and tiller density in any of the species. The birth rate of *F. rubra* tillers was negatively related to their density. An increase in death rate of *F. rubra* tillers lead to an increase in their birth rate. The frequency of flowering in *F. rubra* was negatively related to its density. Negative relationships were found between spring temperature and the death rates of *F. rubra* and *P. irrigata* tillers. The birth rates of tillers of all species were positively related to summer precipitation.

Key-words: *Agrostis stolonifera*, *Festuca rubra*, *Poa irrigata*, population regulation, tiller population, weather effects.

INTRODUCTION

Much attention has been focused on characterizing the factors involved in regulating ramet populations. Evidence for density-dependent regulation has been found in experimental populations of grasses (e.g. Langer *et al.* 1964; Kays & Harper 1974). It is, however, still unclear how populations in natural field situations are regulated.

A negative relationship between ramet density and production of new ramets has been found for many species of herbs and grasses (e.g. Putwain *et al.* 1968; Barkham 1980; Thompson & Beattie 1981; Lapham & Drennan 1987; Briske & Butler 1989), while a density-related increase in the mortality of ramets has rarely been found (Lovett Doust 1981). Instead, weather fluctuations have been suggested to be the major cause of variation in ramet mortality (Fowler 1986; Lapham & Drennan 1987; Briske & Butler 1989).

This paper deals with the effects of intra- and inter-specific density, precipitation and temperature on tiller (ramet) survival and on the production of new tillers in natural populations of *Agrostis stolonifera* L., *Festuca rubra* L. and, *Poa irrigata* Lindm. (= *Poa pratensis* ssp. *irrigata*).

MATERIALS AND METHODS

The field investigation was carried out on part of the Baltic seashore meadow at Tullgarnsnä set, 60 km SW of Stockholm, Sweden. The most common plant species in the

Present address: Icelandic Museum of Natural History, P.O. Box 5320, 15-125 Reykjavik, Iceland.

meadow are *Juncus gerardii* Lois., *Festuca rubra*, *Agrostis stolonifera*, *Poa irrigata* and *Potentilla anserina* L. all clone-forming species and the non-clonal *Plantago maritima* L. The meadow is grazed by cattle throughout the summer. A detailed description of the study area is given in Wallentinus (1973).

The three investigated grass species are all perennial grasses. *A. stolonifera* is loosely to rather densely tufted, sometimes mat-forming, and produces intra- or extra-vaginal shoots which sometimes develop up to 2 m long branched or unbranched stolons (Widén 1971). *F. rubra* is morphologically highly variable. In the investigated area it is densely tufted or mat-forming, with numerous closely packed tillers and short, slender rhizomes. *P. irrigata* has scattered solitary tillers or small tufts of tillers growing from slender, extensively creeping rhizomes. The tiller demography of the investigated species has been described by Jónsdóttir (1991) who found that the tiller populations are maintained by vegetatively produced tillers, which are produced continually throughout the growing season (May–September). Moreover, of the three species studied here, *A. stolonifera* has the most short-lived tillers, with a maximum age of about 3 years. Tillers of *F. rubra* and *P. irrigata* have a maximum age of 4–5 years and a little lesser than 4 years respectively (Jónsdóttir, 1991).

The field data were obtained from repeated mappings of 16 permanent (1 dm × 1 dm) plots. Ten of the plots were established in June 1982, and the other six were added in early June 1983. Each plot was mapped three to five times per year during 1982–1985 and twice in 1986. The analyses were based on three mappings per year: just after growth started in May ('spring') during the flowering period in July ('summer') and at the end of the season in late September or early October ('autumn'). No autumn mapping was made in 1983, nor was a July mapping made in 1986.

All grass tillers were marked with a coloured piece of straw at the beginning of the study. On each following mapping occasion, tillers were identified by their position and marking colour, and new tillers were marked with a new colour. Each tiller was followed until it died or until the study ended. All ramets of species other than the investigated grasses were counted on each mapping occasion.

Inter- and intraspecific density and rates of birth and death of tillers were calculated per plot for each species and census period. Density was measured as number of tillers or ramets per plot (Table 1). To allow comparison of periods of different lengths, daily rates of birth and death were calculated as the percentage tillers born or dead per day during a census period and the number of tillers alive at the beginning of the period.

Multiple regression was used to assess the effects of inter- and intraspecific density at time $t-1$ and the death rates of tillers at times t and $t-1$ on the rate of tiller birth at time t (Table 2). Death rate was analysed using the same procedure, to determine its relation to density, and to the birth rates at time t and $t-1$. In addition, the effects of spring temperature and summer precipitation on rates of birth and death of tillers were tested. Temperature was measured as accumulated degrees above zero until the May observation. Precipitation was measured as the lowest moving average of 21 days (daily) precipitation (Fig. 1).

To determine the degree to which years and plots explained the variation in rates of birth and death, the years and plots were used in the regressions as indicator variables (dummy variables 'Table 2' Zar 1974; Draper & Smith 1981). Only one weather variable was available for each period per year (the same for all plots). Therefore, analyses could not be run with both *year* (indicator variable) and the weather variables simultaneously. When the weather variable was left in the final model, ANOVA (Sokal & Rohlf 1981) was

Table 1. Number of plots in which *Agrostis stolonifera*, *Festuca rubra* and *Poa irrigata* occurred and intra- and interspecific density (range in the numbers of tillers/ramets per plot) for each species at each observation time

	<i>Agrostis stolonifera</i>		<i>Festuca rubra</i>		<i>Poa irrigata</i>	
	Number of plots	Intra-(inter-) specific density	Number of plots	Intra-(inter-) specific density	Number of plots	Intra-(inter-) specific density
<i>1982</i>						
Summer	7	5-86(23-106)	6	30-104(15-66)	2	5-6(105-110)
Autumn	7	6-110(17-124)	6	35-142(15-66)	2	5-6(110-157)
<i>1983</i>						
Spring	8	5-143(14-124)	6	5-156(14-64)	2	6-9(128-170)
Summer	11	5-126(16-210)	11	9-156(22-84)	6	5-25(121-214)
<i>1984</i>						
Spring	9	9-51(10-121)	11	7-134(23-66)	6	7-22(119-179)
Summer	10	7-76(10-99)	12	11-92(20-94)	5	5-17(55-122)
Autumn	12	6-101(8-172)	13	8-112(17-104)	5	9-26(81-179)
<i>1985</i>						
Spring	13	6-101(6-175)	13	12-136(17-106)	5	9-41(82-183)
Summer	12	7-93(10-173)	13	12-120(28-107)	5	8-39(91-180)
Autumn	12	11-93(10-145)	13	16-158(33-112)	5	8-40(120-195)
<i>1986</i>						
Spring	11	15-99(5-126)	13	27-169(17-100)	5	6-32(119-196)

Table 2. List of variables used in regression analyses. Each dependent variable (a) was run against each independent variable (a) and each dependent variable (b) was run against each independent variable (b). IND=indicator (dummy) variables, *analyses were run with only one of these variables simultaneously

Dependent variable	Independent variable
(a) Birth rate at time t	(a) Death rate at time t
	(a) Death rate at time $t-1$
	(ab) Intraspecific density at time $t-1$
	(ab) IND <i>year</i> *
	(ab) precipitation*/temperature*
	(ab) IND <i>plot</i>
(b) Death rate at time t	(ab) Interspecific density at time $t-1$
	(b) Birth rate at time $t-1$
	(b) Birth rate at time t

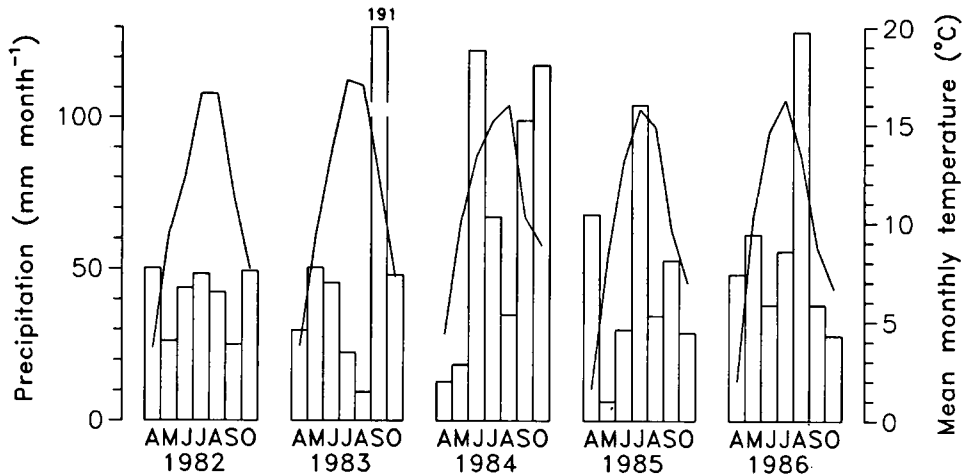


Fig. 1. The monthly precipitation (bars) and temperature (curves) during the vegetation periods 1982–1986.

used to evaluate the effect of different years. The rates of birth and death of tillers were arcsin transformed (Zar 1974) to fulfill the assumption of normality.

The variables explaining a significant amount of variation in birth or death rates were identified by a stepwise elimination procedure starting with all variables included. Only those variables that contributed significantly to the explanation were included in the final model. In some cases more than one regression model explained a significant amount of the variation in rates of birth and death of tillers within the same period. Only significant results are shown and discussed.

The relationships between intraspecific density per plot during the flowering period (July density) and the number of flowering tillers per plot were analysed by Kendall rank correlation (Sokal & Rohlf 1981) in the populations of *A. stolonifera* and *F. rubra* for all years combined. There were not enough data on *P. irrigata* to make such an analysis meaningful.

RESULTS

The birth and death rates of tillers of *A. stolonifera*, *F. rubra* and *P. irrigata* varied within years as well as between years (Table 3). In all three species the lowest rates occurred during spring.

The regression analyses yielded the following results (Table 4):

Agrostis stolonifera. The birth rate of tillers during 'spring' (between autumn last year and spring this year) was positively associated with the death rate during the autumn (between summer and autumn) the year before (time $t-1$). During 'summer' the birth rate was positively related to precipitation.

Festuca rubra. The birth rate of tillers during 'spring' and 'summer' increased along with the death rate in the previous period (autumn the year before and current spring respectively) and during 'autumn' it was positively related to autumn death rate. During 'summer' and 'autumn' the birth rate decreased with increasing intraspecific density. Furthermore, it decreased with decreasing summer precipitation.

The death rate of tillers during 'springs' was positively related to the spring birth rate and decreased with increasing spring temperature.

Table 3. Average birth and death rates (% day⁻¹) per plot for tillers of *Agrostis stolonifera*, *Festuca rubra* and *Poa irrigata* during each observation period. Number of plots given in Table 1

	<i>Agrostis stolonifera</i>		<i>Festuca rubra</i>		<i>Poa irrigata</i>	
	Birth rate	Death rate	Birth rate	Death rate	Birth rate	Death rate
1982						
Summer	1.58	0.48	0.62	0.14	0.00	0.00
Autumn	0.66	0.48	0.73	0.39	0.85	0.16
1983						
Spring	0.13	0.15	0.11	0.10	0.12	0.39
Summer	0.18	0.71	0.08	0.40	0.17	0.17
1984						
Spring*	0.24	0.21	0.12	0.20	0.05	0.17
Summer	1.50	0.62	0.76	0.30	0.93	0.19
Autumn	0.91	0.54	0.61	0.25	0.60	0.18
1985						
Spring	0.13	0.17	0.51	0.07	0.01	0.05
Summer	0.75	0.69	0.45	0.29	0.19	0.21
Autumn	0.98	0.68	0.88	0.52	0.28	0.70
1986						
Spring	0.21	0.22	0.11	0.16	0.07	0.14

*Because no autumn observation was made in 1983, tillers that were born or that died during that period are included in these values.

Poa irrigata. The birth rate of tillers during 'summer' increased with increasing precipitation. The death rate of tillers during 'spring' was negatively related to spring temperature, and differed significantly between years.

Year explained a significant amount of the variation in the birth rate in *A. stolonifera*, *F. rubra* and *P. irrigata* during 'summer' (ANOVA, $F_{(3,36)} = 16.05$, $P_F < 0.001$, $F_{(3,38)} = 18.15$, $P_F < 0.001$ and $F_{(3,15)} = 5.35$, $P_F = 0.011$ respectively). *Year* also explained a significant amount of the variation in death rate of *F. rubra* and *P. irrigata* tillers during 'spring' (ANOVA, $F_{(3,40)} = 8.64$, $P_F = 0.001$ and $F_{(3,12)} = 6.28$, $P_F = 0.019$ respectively).

No significant relationships were found between interspecific density and rates of birth and death in any of the species.

The coefficients of determination were rather low in most cases.

Significant relationships were not found between the frequency of flowering and intra-specific density in *A. stolonifera*, whereas in *F. rubra*, frequency of flowering was negatively related to density (Kendall rank correlation coefficient = 0.20, $P = 0.038$, $n = 96$).

DISCUSSION

The studied species did not recruit from seedlings during the study period (Jónsdóttir 1991). Therefore, population density reflect the balance between the rate of emergence

Table 4. Significant results of multiple regression analyses relating dependent variables = Y (rates of birth and death (arcsin transformed) at time t of *Agrostis stolonifera*, *Festuca rubra* and *Poa irrigata* tillers) to the independent variables = X (interspecific density, intraspecific density, temperature in spring, precipitation in Summer), indicator (dummy) variables = Z (*year* and *plot*). Furthermore, the deaths rate at times t and $t-1$ were used as independent variables in regressions against birth rate as dependent variable, and birth rates at times t and $t-1$ were related to death rate as dependent variable. Only those independent variables who contributed significantly to the final model are included in each model. P_F of the final model and coefficients of determination (r^2) adjusted for degrees of freedom are shown

Species			P_F	r^2
<i>Agrostis stolonifera</i>				
	Formula: $Y = a + bX_1$			
	Variable	Spring birth rate (t)	Autumn death rate ($t-1$)	
	Coefficient	0.0233	0.2226	$P_{F(1.27)} = 0.021,$ 0.15
	Variable	Summer birth rate (t)	Precipitation	
	Coefficient	0.0277	0.4726	$P_{F(1.38)} = 0.002,$ 0.21
<i>Festuca rubra</i>				
	Formula: $Y = a + bX_1$			
	Variable	Spring birth rate (t)	Autumn death rate ($t-1$)	
	Coefficient	0.0029	0.4067	$P_{F(1.30)} < 0.001,$ 0.36
	Variable	Summer birth rate (t)	Precipitation	
	Coefficient	0.0238	0.2934	$P_{F(1.40)} = 0.004,$ 0.17
	Formula: $Y = a + bX_1 + cX_2$			
	Variable	Summer birth rate (t)	Intraspecific density ($t-1$)	Spring death rate ($t-1$)
	Coefficient	0.053	-0.0003	0.931
				$P_{F(2.27)} = 0.008,$ 0.25
	Variable	Autumn birth rate (t)	Intraspecific density ($t-1$)	Autumn death rate (t)
	Coefficient	0.0751	-0.0002	0.3706
				$P_{F(2.29)} = 0.015$ 0.20
	Formula: $Y = a + bX_1 + \alpha Z_1 + \beta Z_2$			
	Variable	Autumn birth rate (t)	Intraspecific density ($t-1$)	<i>year year</i>
	Coefficient	0.1007	-0.0002	-0.0131 0.0046
				$P_{F(3.28)} = 0.008,$ 0.27
	Formula: $Y = a + bX_1 + cX_2$			
	Variable	Spring death rate (t)	Spring birth rate (t)	Temperature
	Coefficient	0.0301	0.4599	-0.0001
				$P_{F(2.29)} = 0.002,$ 0.31
<i>Poa irrigata</i>				
	Formula: $Y = a + bX_1$			
	Variable	Summer birth rate (t)	Precipitation	
	Coefficient	-0.0253	0.5565	$P_{F(1.16)} = 0.007,$ 0.34
	Variable	Spring death rate (t)	Temperature	
	Coefficient	0.0607	-0.0002	$P_{F(1.10)} = 0.028,$ 0.34

of new tillers and tiller survival. The fact that rates of birth and death of ramets have commonly been found to vary in a synchronized way in clonal plant species (e.g. Noble *et al.* 1979; Lovett Doust 1981; Newell *et al.* 1981; Fetcher & Shaver 1983) suggests that causal relationships exist between these two demographic processes. In this regard, synchronization could be mediated by competition between individual ramets for resources in the habitat, or alternatively, it could reflect centralized control within the clone (e.g. Cook 1985; Hutchings & Bradbury 1986).

The negative relationships found between the intraspecific density and birth rate of tillers of *F. rubra* agree with the results of several other studies on clonal plants (Putwain *et al.* 1968; Barkham 1980; Thompson & Beattie 1981; Lapham & Drennan 1987; Briske & Butler 1989). These relationships, together with the fact that the increase in birth rate lagged behind the increase in death rate, provide strong evidence that already established tillers of *F. rubra* regulate the production of new tillers in crowded habitats. Furthermore, the finding that the flowering frequency in *F. rubra* tillers was negatively related to the density of its tillers indicates that as tiller density increases, their ability to produce new tillers and to flower decreases, presumably as a result of growth inhibition. Thus fewer tillers reach the physiological stage at which they are able to produce daughter tillers and flowers.

No evidence was found indicating that the death rates of tillers of *A. stolonifera*, *F. rubra* and *P. irrigata* are related to tiller density. Nor was there any evidence that the tiller mortality rate depended on the rate of tiller births. It has been suggested that integration among ramets of a clone reduce the competition to levels below the threshold for ramet mortality (Hutchings & Bradbury 1986).

The density of *F. rubra* in the investigated area was higher than of that *A. stolonifera* or *P. irrigata*. Density effects were therefore more likely to be found in *F. rubra* than in the other two species. Intraspecific effects may occur within or between clones in clonal plants. In view of the clonal growth habit of *F. rubra*, one might expect that intraclonal interferences between tillers is common in this species. Interpretation of the results of this study is limited by the fact that the clonal identities, developmental programs of the clones and the degree of interconnection between tillers of *A. stolonifera*, *F. rubra* and *P. irrigata* were not known. Thus without further investigations, it will not be possible to determine whether the relationships found between the density and birth rate of *F. rubra* tillers are controlled at the level of individual tiller or group of interconnected tillers.

The effects of weather fluctuations on reproduction and seed set have been analysed in several studies (Inghe & Tamm 1985; Rabinowitz *et al.* 1989), but few attempts have been made to relate variation in survival and growth to weather factors, although weather fluctuations have sometimes been suggested to be, at least partly responsible for ramet mortality (Fowler 1986; Lapham & Drennan 1987; Briske & Butler 1989). Results of the present study indicate that temperature during spring influences the survival of *F. rubra* and *P. irrigata* tillers and that the amount of precipitation during summer affects emergence of new tillers in all three of the investigated species. Unexpected dry periods during summer did not cause a decrease in tiller survival, and the hypothesis that weather explains much of the variation in death rate was not supported by the results. In most cases the observed variation in rates of birth and death was explained better by *year* than by the weather variables. This suggests importance of unstudied abiotic factors and interactions between different factors in determining production of new tillers and tiller survival in the study's species.

ACKNOWLEDGEMENTS

I thank Ove Eriksson for comments on the manuscript and Ola Inghe for help with the statistical analyses.

REFERENCES

- Barkham, J.P. (1980): Population dynamics of the wild daffodil (*Narcissus pseudonarcissus*). I. Clonal growth, seed reproduction, mortality and the effects of density. *J. Ecol.* **69**: 607–633.
- Briske, D.D. & Butler, J.L. (1989): Density-dependent regulation of ramet populations within the bunchgrass *Schizachyrium scoparium*: Interclonal versus intraclonal interference. *J. Ecol.* **77**: 693–974.
- Cook, R.E. (1985): Growth and development in clonal plant populations. In: Jackson, J.B.C., Buss, L.W. and Cook, R.E. (eds): *Population Biology and Evolution of Clonal Organisms*, 259–296. Yale University Press, New Haven.
- Draper, N. & Smith, H. (1981): *Applied Regression Analysis*, 2nd edn. John Wiley & Sons, New York.
- Fetcher, N. & Shaver, G.R. (1983): Life histories of tillers of *Eriophorum vaginatum* in relation to tundra disturbance. *J. Ecol.* **71**: 131–147.
- Fowler, N. (1986): Density-dependent population regulation in a Texas grassland. *Ecology* **67**: 545–554.
- Hutchings, J.M. & Bradbury, I.K. (1986): Ecological perspectives on clonal perennial herbs. *BioScience* **36**: 178–182.
- Inghe, O. & Tamm, C.O. (1985): Survival and flowering of perennial herbs V. Patterns of flowering. *Oikos* **51**: 203–219.
- Jónsdóttir, G.Á. (1991): Tiller demography in seashore populations of *Agrostis stolonifera*, *Festuca rubra* and *Poa irrigata*. *Journal of Vegetation Science* **2**: 89–94.
- Kays, S. & Harper, J.L. (1974): The regulation of plant and tiller density in grass sward. *J. Ecol.* **62**: 97–105.
- Langer, R.H.M., Ryle, S.M. & Jewiss, O.R. (1964): The changing plant and tiller populations of Timothy and meadow fescue swards. I. Survival and the pattern of tillering. *J. Appl. Ecol.* **1**: 197–208.
- Lapham, K.J. & Drennan, D.S.H. (1987): Intraspecific regulation of populations of the clonal herb *Cyperus esculentus*. *J. Appl. Ecol.* **24**: 1011–1024.
- Lovett Doust, L. (1981): Population dynamics and local specialization in clonal perennial (*Ranunculus repens*). I. The dynamics of ramets in contrasting habitats. *J. Ecol.* **69**: 743–755.
- Newell, S.J., Solbrig, O.T. & Kincaid, D.T. (1981): Studies on the population biology of the genus *Viola*. III. The demography of *Viola blanda* and *Viola pallescens*. *J. Ecol.* **69**: 997–1016.
- Noble, J.C., Bell, A.D. & Harper, J.L. (1979): The population biology of plants with clonal growth. I. The morphology and structural demography of *Carex arenaria*. *J. Ecol.* **67**: 983–1008.
- Putwain, P.D., Machin, D. & Harper, J.L. (1968): Studies of the dynamics of plant populations. 2. Components of regulation of a natural population of *Rumex Acetosella* L. *J. Ecol.* **56**: 421–431.
- Rabinowitz, D., Rapp, J.K., Cairns, S. & Mayer, M. (1989): The persistence of rare prairie grasses in Missouri: Environmental variation buffered by reproductive output of sparse species. *Am. Nat.* **134**: 525–544.
- Sokal, R.R. & Rohlf, F.J. (1981): *Biometry*. Freeman, San Francisco.
- Thompson, D.A. & Beattie, A.J. (1981): Density mediated seed and stolon production in *Viola* (Violaceae). *Amer. J. Bot.* **68**: 383–388.
- Wallentinus, H.-G. (1973): Description of sea-shore meadow communities, with special reference to the *Juncetum gerardii*. The sea-shore meadows of the Tullgarnsnä set IV. *Sv. Bot. Tidskr.* **67**: 401–422.
- Widén, K.G. (1971): The genus *Agrostis* L. in eastern Fennoscandia. Taxonomy and distribution. *Flora Fennica* **5**.
- Zar, J.H. (1974): *Biostatistical analysis*. Prentice Hall, New York.