The Demography of Bromus Tectorum: The Role of Microclimate, Grazing and Disease
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THE DEMOGRAPHY OF *BROMUS TECTORUM*: THE ROLE OF MICROCLIMATE, GRAZING AND DISEASE

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SUMMARY

(1) Correlations between weather and the emergence of cohorts and correlation between weather, disease and grazing and subsequent cohort survivorship were investigated for the introduced annual *Bromus tectorum* in three habitat types in eastern Washington, U.S.A., for three consecutive generations.

(2) Emergence of twenty out of twenty-four cohorts among the three sites in late summer to early autumn closely followed showers; emergence in spring could be related less commonly with isolated showers.

(3) Emergence in winter probably did not occur until soil surfaces were free of snow and air temperatures were at or above 0 °C; spring emergence was less predictable but occurred even as available soil moisture progressively declined.

(4) Many members of cohorts emergent in late summer and early autumn at all three sites were often killed by drought in September and October.

(5) In winter, plants, regardless of age, were disturbed by frost-heaving at the moist and mesic sites; grazing by voles was common under snow cover.

(6) Infestation by *Ustilago bullata* was most common at the mesic site.

(7) The abundance and distribution of *Bromus tectorum* seem to be determined by the chronology of environmental events.

INTRODUCTION

Custom seemingly has caused autecologists and population ecologists to develop contrasting perspectives in plant ecology (Harper 1967). Autecologists emphasize accurate measurement of the physical environment, while often using the performance (e.g. in g m^{-2} $year^{-1}$) of a small number of even-aged plants as an accurate indicator of the behaviour of a population in nature. Alternatively, population ecologists recognize populations as always dynamic and as usually mixed-age groups of organisms but often only superficially quantify the source of much change, the physical environment (Mooney 1976). Moreover, correlations between environmental changes and phenologic events such as germination are rarely related to demography (Weiss 1981; Klemow & Raynal 1983). Few studies of mortality with deaths partitioned by cause, comparable to those compiled for the control of insects (Morris & Miller 1954), have been completed for plants (Steenbergh & Lowe 1969; Gashwiler 1971; Watkinson & Harper 1978). Understanding is clearly weakened in both autecology and population ecology by failure to incorporate the complementary approach. Benefits garnered from a synthetic approach have been recognized (Raven 1979) but seldom realized (e.g. Regehr & Bazzaz 1979; Black & Bliss 1980).

Since its introduction in the late 19th century (Mack 1981a), *Bromus tectorum* L. (downy brome, cheatgrass) has become a dominant in many steppe communities between the Sierra Nevada and the Rocky Mountains in western North America. We attempt here to relate specific events (e.g. frost-heaving, herbivory, the distribution and form of precipitation) from August to the following June with the pattern of recruitment and survival for this grass in the steppe of eastern Washington (U.S.A.). *Bromus tectorum* is ideal for such examination because: (i) all vegetative growth occurs during only one annual cycle of weather; (ii) with recruitment often spanning 8 months (Mack & Pyke 1983), effects of environmental events on different-aged cohorts may also be studied; (iii) mortality may be compared among non-overlapping generations in consecutive years; (iv) earlier reports suggest a relation between episodes of autumn precipitation and recruitment (Hulbert 1955; Beatley 1966). For comparison with this demographic approach an attempt was made to relate these same environmental events with standing crop and density in June.

At each of three habitat types across a 200-km moisture gradient (Daubenmire 1970), the demography of *Bromus tectorum* was followed for three consecutive generations. Using the habitat classification of Daubenmire (1970), a moist site in Whitman County was within the *Festuca idahoensis-Symphoricarpos albus* habitat type. A mesic study site was in the *Agropyron spicatum-Festuca idahoensis* habitat type near Hooper in Whitman County, while our study site at the dry end of this gradient was within the *Artemisia tridentata-Agropyron spicatum* habitat type on the Arid Lands Ecology Reserve in Benton County. Further details of these habitats are given in Mack & Pyke (1983).

METHODS

Germination was followed at five temperatures (°C ± range)—<0 ± 1, 3 ± 1, 4 ± 1, 6 ± 2, 12 ± 2—for 30 days. Seed lots (99% germination at room temperature in 1983), each of 100 seeds collected at the moist site in 1979, were sown onto moistened germination pads in a refrigerated seed germinator with continuous illumination. New seedlings were moved daily.

Seedlings in nature were mapped by the technique of Mack & Pyke (1983). Censuses were conducted in 40 × 50 cm plots; there were five plots at each of the moist and mesic sites and eight plots at the dry site. Censuses were 3–4 weeks apart and dead or damaged plants could often be placed into categories, including those infected with *Ustilago bullata* Berk., and those killed by desiccation or by trampling. Deaths were attributed to grazing for plants that had more than 25% of the foliage removed between two consecutive censuses. We were often unable to discriminate between death caused by frost-heaving, burial under snow or exposure to temperatures below 0 °C, hence we use the category, winter death. All plants infected with smut were considered dead at harvest in June. The withered remains of the plant were found for each death from drought; no cause of death was assigned for plants that were simply missing. In early June all *Bromus tectorum* individuals on a plot were harvested at ground level, dried (48 h at 100 °C), and weighed. Frequent mapping, and harvesting in June, were repeated in the same plots at each site for the 3 years of the study. The generations followed at each site during 1977–78, 1978–79 and 1979–80 will be referred to as the first, second and third year populations, respectively.

Annual contribution to the litter layer in these plots was estimated by bulk harvesting, drying (48 h at 100 °C) and weighing the standing-dead crop in June 1981. Plant remains in rabbit faeces from the plots at the dry site were identified by the Washington State University Wildlife Habitat Laboratory. Small mammalian grazers were identified by trapping near the plots.

In October 1979 a micrometeorological station was established at each site. Variables measured at 1 m above the soil surface (and sensors used) were: mean ($kJ\ m^{-2}\ min^{-1}$) and maximum (kJ m^{-2}) daily solar radiation (Lambda Instruments LI-200S pyranometer); maximum, minimum and average daily air temperature (°C) (Fenwal UUT 51J1 thermistor); average daily wet bulb temperature (°C) (Fenwal UUT 51J1 thermistor). Total daily precipitation (mm) (Edmund Scientific digital rain gauge) was measured at 25 cm above the soil surface. Data from all sensors were stored in the field on magnetic tape (Campbell Scientific CR21 Micrologger).

In lieu of meteorological information from the dry site (altitude 446 m) for August to June 1977–78 and 1978–79, data were used from the Hanford Meteorological tower (altitude 223 m), 21 km to the NNE. Meteorological information (U.S. Environmental Data & Information Service 1977–80) from La Crosse (altitude 450 m) 22 km NE of the mesic site (altitude 360 m) and from Pullman (altitude 775m), 8 km SE of the moist site (altitude 830 m), was used for this same period. Data for snow cover were used from these stations for all 3 years.

The daily available moisture at each site was estimated for all thirty-four months of the study by incorporation of field measurements of daily precipitation, average daily short-wave radiation and average daily temperature into expressions developed by Campbell (1977) and Campbell & Harris (1977). In these expressions the soil profile was divided into a shallow layer (0–10 cm) including the rooting depth of seedlings less than 1 month old, and a lower layer (11–60 cm) within the root zone of plants more than 1 month old. When field measurements of daily incoming solar radiation were unavailable, they were calculated using the daily amount of radiation incident on a horizontal surface above the earth's atmosphere (G_h) (Gates 1980). To calculate G_h we followed the procedure of Bristow & Campbell (1982) in using daily temperature extremes and the occurrence of precipitation to estimate daily average transmittance of total shortwave radiation by the atmosphere.

A test of homogeneity was used for analysis of the mortality at each site for each year of the study. The analysis examined, in order, the distribution of total mortality between cohorts and the sources of mortality, the homogeneity among sources of mortality within each cohort, and established a ranking of importance of the sources of mortality for all possible pair-wise comparisons between mortality sources within each cohort.

RESULTS

Seed germination at low temperature

Reduction of air temperature brought about a corresponding delay in the first occurrence of germination. Germination occurred by day 6 for seeds maintained at 12 ± 2 °C but was not detected until day 10 at 0 °C to −1 °C, where the temperature was below 0 °C for at least 6 h per day.

Recruitment

During the 3 years of study, twenty of the twenty-four cohorts emergent before 1 November were first detected within 1 week after rain (Figs 1–9). Occasionally our census schedule permitted detection within 1 day after rain (e.g. the 31 October 1978 cohort at the moist site and the 4 October 1978 cohort at the dry site; Figs 2 & 8). Each shower in late summer and early autumn usually deposited less than 10 mm of precipitation and rain often fell on several days. Emergence of *Bromus tectorum* closely followed even isolated couplets of storms with each shower delivering about 1 mm of rain (e.g. 4 October 1978, cohort at

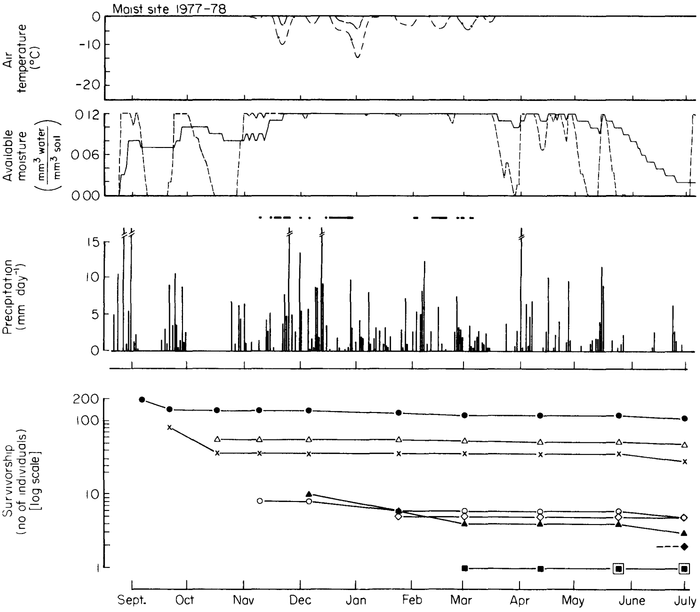

FIG. 1. Composite portrayal of the physical environment and the survival of constituent cohorts of the *Bromus tectorum* population at the moist site in eastern Washington, U.S.A., during 1977–78. (a) Minimum (——) and average (– – –) daily temperatures below 0 °C; (b) estimated daily volume of available moisture per unit volume of soil (mm^3 mm^{-3}) in the 0–10 cm (——) and the 10–60 cm (– – –) soil layers; (c) daily precipitation (mm) and days on which snow was lying are indicated by a horizontal bar across the upper part; (d) survivorship curves for each cohort comprising the population (from Mack & Pyke 1983).

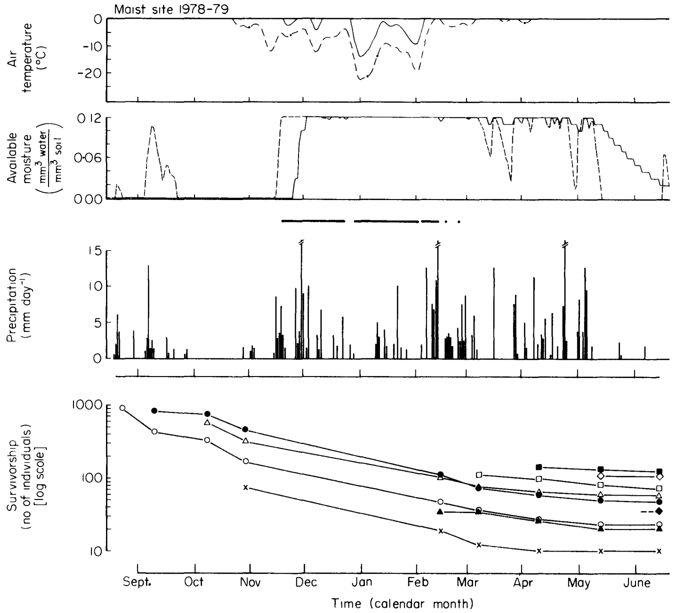

FIG. 2. Composite portrayal of the physical environment and the survival of constituent cohorts of the *Bromus tectorum* population at the moist site in eastern Washington, U.S.A. during 1978–79. Details as in Fig. 1.

TABLE 1. Numbers of dead individuals partitioned by the cause of death in each cohort (as defined by the date of first detected emergence) during 1977–78 for the *Bromus tectorum* population at the moist site in eastern Washington, U.S.A. Within each cohort the numbers of deaths with the same superscript are not significantly different ($P \leqslant 0{\cdot}05$). Interaction between the cohorts and sources of mortality was significantly different ($\chi^2 = 36{\cdot}5$. d.f. = 12, $P \leqslant 0{\cdot}05$). Dashes appear for insufficient deaths to validate the Goodness of Fit test; probability level within a cohort in all tables is $P \leqslant 0{\cdot}05$.

	Cause of death					
Cohort	Desiccation	Smut	Winter death	Unknown	Total	χ^2 (d.f.)
7 September 1977	23^{a}	21^{a}	9^{b}	7^{b}	60	13·3* (3)
22 September 1977	23^{a}	4^{b}	0^{c}	3^{bc}	30	43·9* (3)
18 October 1977	0	5	1	1	7	—
10 November 1977	0	1	2	0	3	—
7 December–25 January 1978	0	1	2	1	4	—
2 March 1978	0	0	0	0	0	
12 April 1978	0	0	0	0	0	
25 May 1978	0	0	0	0	0	
30 June 1978	0	0	0	0	0	
Total	46^{a}	32^{a}	14^{b}	12^{b}	104	29·9* (4)

the dry site; Fig. 8). Recruitment occasionally occurred within virtually rainless periods of several weeks in September and October (e.g. 18 October 1977 at the moist site and the 17 October 1978 cohort at the mesic site; Figs 1 & 5).

Emergence in late winter and early spring 1979 at all sites followed the melting of snow. We could gauge neither the date nor the extent of germination under the snow, although percolating melt water may have enhanced emergence. Additional late winter and early spring recruitment also occurred without a persistent snow cover; emergence was coincident with air temperatures rising to 0 °C or above (e.g. 4 February 1980 cohort at the moist site, the 16 January 1980 cohort at the mesic site, and the 8 January and the 7 February 1980 cohorts at the dry site; Figs 3, 6 & 9).

Recruitment between November and June can not usually be related to specific storms as showers were more frequent than in autumn and the soil continued to hold water above

TABLE 2. Numbers of dead individuals partitioned by the cause of death in each cohort during 1978–79 for the *Bromus tectorum* population at the moist site in eastern Washington, U.S.A. Interaction between cohorts and sources of mortality was significantly different ($\chi^2 = 1928$, d.f. = 32, $P \leqslant 0{\cdot}05$). Details as in Table 1.

	Cause of death						
Cohort	Desiccation	Grazing	Smut	Winter death	Unknown	Total	χ^2 (d.f.)
24 August 1978	708^{a}	6^{cd}	3^{d}	127^{b}	13^{c}	857	2162·9* (4)
11 September 1978	387^{a}	29^{b}	5^{c}	341^{a}	26^{b}	788	909·9* (4)
10 October 1978	253^{a}	10^{b}	9^{b}	231^{a}	19^{b}	522	607·4* (4)
31 October 1978	0^{c}	3^{bc}	2^{bc}	60^{a}	4^{b}	69	194·0* (4)
15 February 1979	0^{b}	0^{b}	2^{b}	0^{b}	14^{a}	16	46·5* (4)
8 March 1979	0^{c}	0^{c}	5^{b}	0^{c}	37^{a}	42	123·9* (4)
18 April 1979	0^{b}	0^{b}	13^{a}	0^{b}	15^{a}	28	42·4* (4)
14 May 1979	0	0	3	0	2	5	—
15 June 1979	0	0	4	0	0	4	—
Total	1348^{a}	48^{d}	46^{d}	759^{b}	130^{c}	2331	2848* (4)

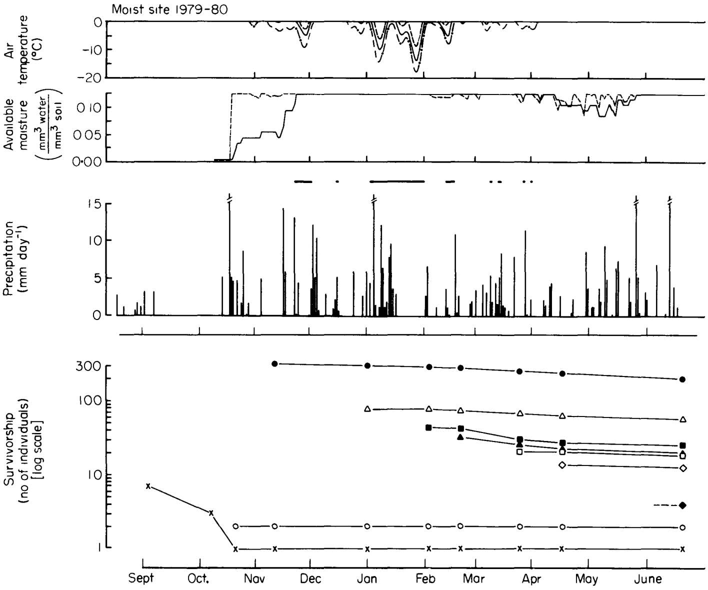

FIG. 3. Composite portrayal of the physical environment and the survival of constituent cohorts of the *Bromus tectorum* population at the moist site in eastern Washington, U.S.A., during 1979–80. Details as in Fig. 1.

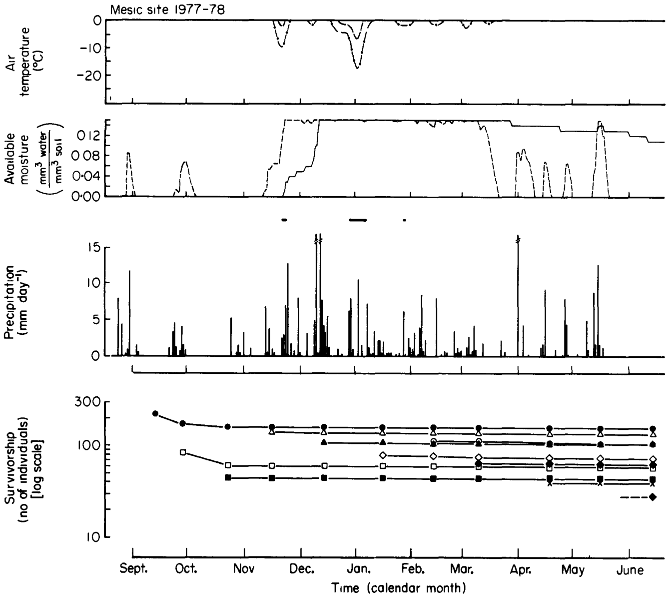

FIG. 4. Composite portrayal of the physical environment and the survival of constituent cohorts of the *Bromus tectorum* population at the mesic site in eastern Washington, U.S.A., during 1977–78. Details as in Fig. 1.

TABLE 3. Numbers of dead individuals partitioned by the cause of death in each cohort during 1979–80 for the *Bromus tectorum* population at the moist site in eastern Washington, U.S.A. Interaction between the cohorts and sources of mortality was significantly different ($\chi^2 = 180{\cdot}5$, d.f. = 12, $P \leqslant 0{\cdot}05$). Details as in Table 1.

	Cause of death						
Cohort	Desiccation	Grazing	Smut	Winter death	Unknown	Total	χ^2 (d.f.)
6 September– 23 October 1979	6	0	1	0	0	7	—
13 November 1979	0^{d}	4^{c}	22^{b}	50^{a}	51^{a}	127	93·5* (4)
2 January 1980	0^{b}	0^{b}	7^{a}	8^{a}	10^{a}	25	17·6* (4)
4 February– 16 April 1980	0^{b}	0^{b}	3^{b}	22^{a}	13^{a}	38	49·1* (4)
Total	6^{c}	4^{c}	33^{b}	80^{a}	74^{a}	197	133·4* (4)

the permanent wilting percentage (e.g. the spring cohorts in the third year population at the moist site; Fig. 3). Available soil moisture occasionally declined in spring so that emergence again followed individual storms and temporary increases in available moisture in the 0–10 cm soil section (e.g. 15 March, 10 April and 9 May 1979 cohorts at the dry site; Fig. 8). The small size of spring cohorts in some years may be due more to the prior depletion of the seed bank (Mack & Pyke 1983) than to restricted moisture.

Sources of mortality

The causes of mortality were not of equal importance within these populations and the percentage of the deaths attributable to each agent varied from year to year. The numbers of deaths were evenly distributed among causes only in the 17 January 1978 cohort at the mesic site (Table 4). The relative importance of different mortality agents was unrelated to features of the sites (Tables 1–9).

In five populations desiccation was the major source of mortality (Tables 1, 2, 4, 6 & 8). Mortality in late summer- or early autumn-emergent cohorts often began only a few weeks after recruitment. Death coincided with consecutive weeks in September and October without rain accompanied by low available soil moisture. The loss of more than 30% of a

TABLE 4. Numbers of dead individuals partitioned by the cause of death in each cohort during 1977–78 for the *Bromus tectorum* population at the mesic site in eastern Washington, U.S.A. Interaction between the cohorts and sources of mortality was significantly different ($\chi^2 = 127{\cdot}7$, d.f. = 21. $P \leqslant 0{\cdot}05$). Details as in Table 1.

	Cause of death					
Cohort	Desiccation	Smut	Winter death	Unknown	Total	χ^2 (d.f.)
14 September 1977	44^{a}	22^{b}	1^{c}	13^{b}	80	49·5* (3)
29 September 1977	23^{a}	6^{b}	0^{c}	0^{c}	29	48·9* (3)
24 October 1977	0	5	0	0	5	—
17 November 1977	0^{b}	11^{a}	0^{b}	4^{a}	15	21·5* (3)
16 December 1977	0^{b}	7^{a}	1^{b}	1^{b}	9	13·7* (3)
17 January 1978	0	4	2	3	9	3·89 N.S. (3)
4 February 1978	0^{b}	10^{a}	0^{b}	7^{a}	17	18·1* (3)
11 March– 14 June 1978	0^{b}	10^{a}	0^{b}	2^{b}	12	22·7* (3)
Total	67^{a}	75^{a}	4^{c}	30^{b}	176	74·7* (3)

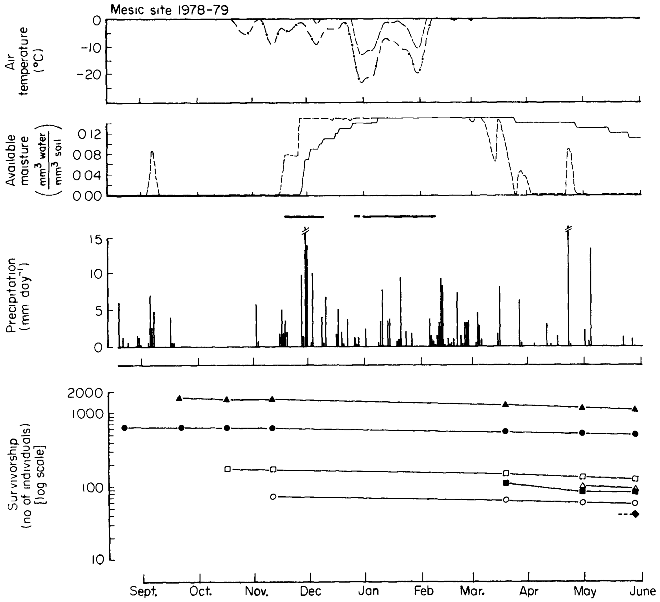

FIG. 5. Composite portrayal of the physical environment and the survival of constituent cohorts of the *Bromus tectorum* population at the mesic site in eastern Washington, U.S.A., during 1978–79. Details as in Fig. 1.

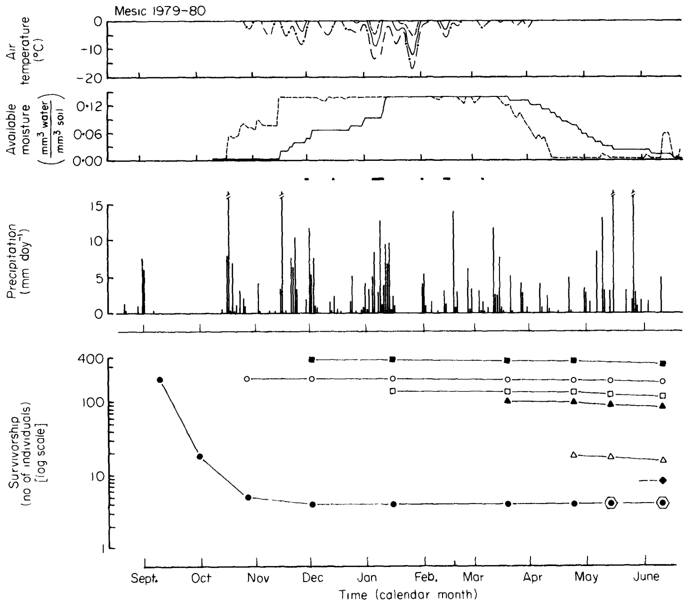

FIG. 6. Composite portrayal of the physical environment and the survival of constituent cohorts of the *Bromus tectorum* population at the mesic site in eastern Washington, U.S.A., during 1979–80. Details as in Fig. 1.

TABLE 5. Numbers of dead individuals partitioned by the cause of death in each cohort during 1978–79 for the *Bromus tectorum* population at the mesic site in eastern Washington, U.S.A. Interaction between the cohorts and sources of mortality was significantly different ($\chi^2 = 100{\cdot}5$, d.f. = 18. $P \leqslant 0{\cdot}05$). Details as in Table 1.

Cohort	Cause of death Desiccation	Smut	Winter death	Unknown	Total	χ^2 (d.f.)
23 August 1978	32^{c}	38^{bc}	69^{a}	57^{ab}	196	17·8* (3)
22 September 1978	67^{d}	101^{c}	275^{a}	172^{b}	615	164·8* (3)
17 October 1978	1^{c}	9^{b}	25^{a}	23^{a}	58	27·2* (3)
13 November 1978	0^{b}	3^{ab}	9^{a}	7^{a}	19	10·3* (3)
19 March 1979	0^{c}	4^{b}	0^{c}	26^{a}	30	62·3* (3)
1 May 1979	0^{b}	8^{a}	0^{b}	7^{a}	15	15·1* (3)
30 May 1979	0	3	0	0	3	—
Total	100^{d}	166^{c}	378^{a}	292^{b}	936	199·5* (3)

cohort often occurred within 30-day spans without rain (e.g. the 6 September 1979 cohort at the moist site and the early autumn-emergent cohorts in the second year at the dry site; Figs 3 & 8, Tables 3 & 8). In contrast, long periods of drought did not always result in many deaths (e.g. the early autumn-emergent cohorts in the second year population at the mesic site; Fig. 5).

Seedling death by desiccation occurred among cohorts emerging before mid-October in eight populations. In nine of thirteen such late summer- or early autumn-emerging cohorts, desiccation in autumn was the major source of death (Tables 1–8). In an extreme example (the 11 September 1979 cohort at the mesic site; Fig. 6, Table 6) 93% of all deaths occurred by desiccation before 29 October. The likelihood of more than 30% of all deaths being caused by desiccation depended on the distribution of autumnal rain rather than type of site or age of seedlings. Drought in September and October usually caused many deaths in all cohorts (e.g. the 24 August, 11 September and 10 October 1978 cohorts at the moist site; Fig. 2, Table 2). Available moisture in the upper 60 cm of soil at all sites commonly declined or widely fluctuated in spring (e.g. the dry site in each spring; Figs 7–9), accounting for some deaths in late spring (e.g. loss in May in cohorts in the third year population at the mesic site; Fig. 6, Table 6).

TABLE 6. Numbers of dead individuals partitioned by the cause of death in each cohort during 1979–80 for the *Bromus tectorum* population at the mesic site in eastern Washington, U.S.A. Interaction between the cohorts and sources of mortality was significantly different ($\chi^2 = 429{\cdot}6$, d.f. = 18, $P \leqslant 0{\cdot}05$). Details as in Table 1.

Cohort	Cause of death Desiccation	Smut	Winter death	Unknown	Total	χ^2 (d.f.)
11 September 1979	198^{a}	0^{c}	1^{c}	13^{b}	212	530·9* (3)
29 October 1979	0^{c}	32^{a}	14^{b}	11^{b}	57	37·1* (3)
3 December 1979	0^{c}	41^{a}	16^{b}	35^{a}	92	45·5*(3)
16 January 1980	0^{c}	20^{a}	5^{b}	16^{a}	41	25·4* (3)
18 March 1980	0^{b}	14^{a}	0^{b}	18^{a}	32	33·0* (3)
23 April 1980	0	4	0	3	7	—
13 May 1980	0	0	0	0	0	—
10 June 1980	0	1	0	0	1	—
Total	198^{a}	112^{b}	36^{c}	96^{b}	442	429·6* (3)

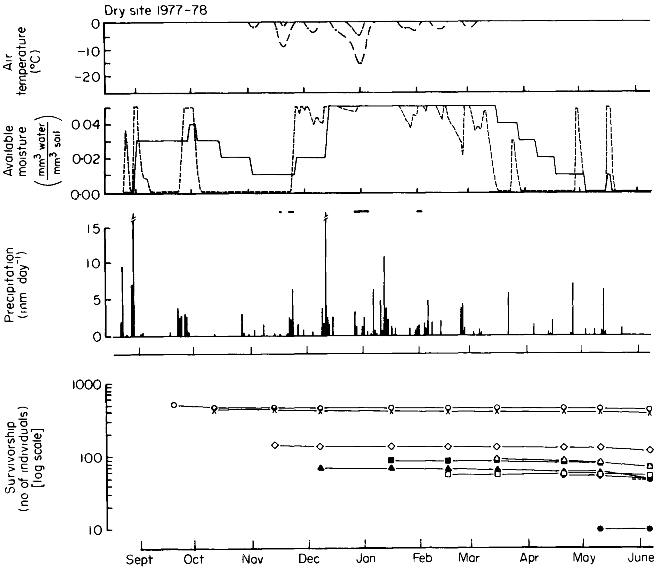

FIG. 7. Composite portrayal of the physical environment and the survival of constituent cohorts of the *Bromus tectorum* population at the dry site in eastern Washington, U.S.A., during 1977–78. Details as in Fig. 1.

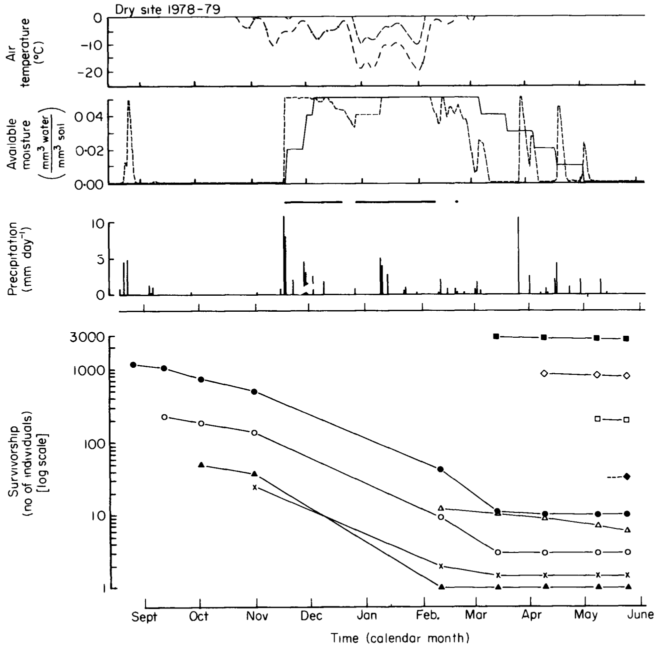

FIG. 8. Composite portrayal of the physical environment and survival of constituent cohorts of the *Bromus tectorum* population at the dry site in eastern Washington, U.S.A., during 1978–79. Details as in Fig. 1.

TABLE 7. Numbers of dead individuals partitioned by the cause of death in each cohort during 1977–78 for the *Bromus tectorum* population at the dry site in eastern Washington, U.S.A. Interaction between cohorts and sources of mortality was significantly different ($\chi^2 = 149{\cdot}2$, d.f. = 18, $P \leqslant 0{\cdot}05$). Details as in Table 1.

	Cause of death					
Cohort	Desiccation	Smut	Winter death	Unknown	Total	χ^2 (d.f.)
20 September 1977	42^{a}	4^{b}	0^{c}	9^{b}	55	80·4* (3)
12 October 1977	6^{c}	0^{d}	16^{b}	32^{a}	54	43·5* (3)
14 November 1977	0^{b}	0^{b}	8^{a}	15^{a}	23	27·3* (3)
9 December 1977	0^{b}	0^{b}	2^{b}	14^{a}	16	34·0* (3)
17 January–17 February 1978	0^{b}	0^{b}	2^{b}	16^{a}	18	39·8* (3)
16 March 1978	0^{b}	0^{b}	0^{b}	18^{a}	18	54·0* (3)
21 April 1978	0	0	0	6	6	—
11 May 1978	0	0	0	0	0	—
7 June 1978	0	0	0	0	0	—
Total	48^{b}	4^{d}	28^{c}	110^{a}	190	130·1* (3)

Infection with *Ustilago bullata* usually first appeared in the developing inflorescence. Smut infected plants in all populations, although spring- and winter-emergent cohorts occasionally were not infected (e.g. the winter and spring cohorts at the moist and dry sites in 1977–78; Figs 1 & 7). Smut caused more than 30% of all deaths in spring-emergent cohorts more often than in late-summer and autumn-emergent cohorts. Plants at the mesic site were the most susceptible to fungal attack, i.e. frequency of infestation (twenty-one of twenty-three cohorts) and the likelihood of that infestation contributing to more than 30% of all deaths (twelve of twenty-three cohorts; Tables 4–6). In contrast, at the moist site and the dry site only six of twenty-two (Tables 1–3) and six of twenty-three cohorts (Tables 7–9), respectively, were similarly devastated by smut. Smut accounted for less than 30% of all deaths in cohorts in the third year population at the moist site and in the first year population at the dry site.

Winter death occurred in all populations but was restricted to cohorts emergent before the frost-free season in spring. The latest-emergent cohort to lose members by winter death was first detected on 4 February 1980 at the moist site (Table 3). The likelihood of winter

TABLE 8. Numbers of dead individuals partitioned by the cause of death in each cohort during 1978–79 for the *Bromus tectorum* population at the dry site in eastern Washington, U.S.A. Interaction between the cohorts and sources of mortality was significantly different ($\chi^2 = 2772$, d.f. = 28, $P \leqslant 0{\cdot}05$). Details as in Table 1.

	Cause of death						
Cohort	Desiccation	Grazing	Smut	Winter death	Unknown	Total	χ^2 (d.f.)
28 August 1978	677^{a}	0^{c}	1^{c}	493^{b}	1^{c}	1172	1828* (4)
14 September 1978	87^{b}	0^{c}	0^{c}	134^{a}	0^{c}	221	356·5* (4)
4 October 1978	13^{b}	0^{c}	0^{c}	36^{a}	0^{c}	49	100·5* (4)
2 November 1978	0^{b}	0^{b}	0^{b}	25^{a}	0^{b}	25	100·0* (4)
20 December–12 February 1979	0	0	0	2	4	6	—
15 March 1979	0^{d}	4^{c}	107^{b}	0^{d}	213^{a}	324	553·1* (4)
11 April 1979	0^{c}	0^{c}	33^{b}	0^{c}	74^{a}	107	199·8* (4)
10 May 1979	0^{b}	0^{b}	9^{a}	0^{b}	7^{a}	16	24·6* (4)
Total	777^{a}	4^{e}	150^{d}	690^{b}	299^{c}	1920	1183·5* (4)

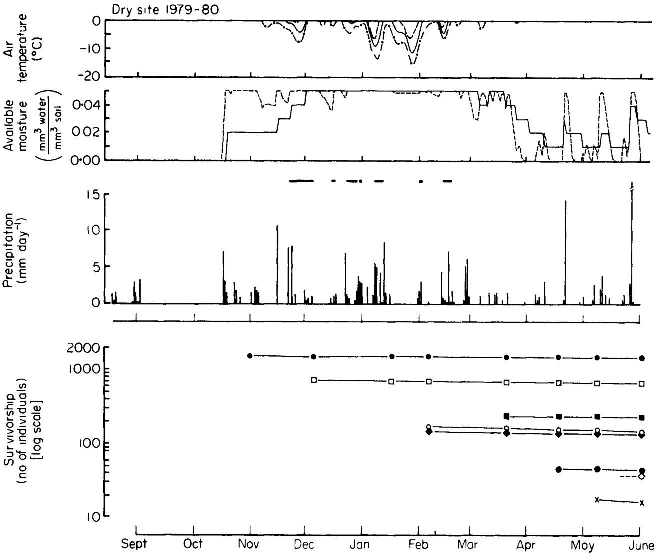

FIG. 9. Composite portrayal of the physical environment and survival of constituent cohorts of the *Bromus tectorum* population at the dry site in eastern Washington, U.S.A., during 1979–80. Details as in Fig. 1.

TABLE 9. Numbers of dead individuals partitioned by the cause of death in each cohort during 1979–80 for the *Bromus tectorum* population at the dry site in eastern Washington, U.S.A. Interaction between the cohorts and sources of mortality was significantly different (χ^2 = 27·9, d.f. 15, $P \leqslant 0{\cdot}05$). Details as in Table 1.

	Cause of death					
Cohort	Grazing	Smut	Winter death	Unknown	Total	χ^2 (d.f.)
2 November 1979	7^b	48^a	11^b	43^a	109	49·6* (3)
7 December 1979	6^b	22^a	2^b	35^a	65	42·6* (3)
18 January 1980	0^b	11^a	0^b	19^a	30	34·3* (3)
7 February 1980	2^b	3^b	0^b	20^a	25	41·1* (3)
20 March 1980	0^b	2^{ab}	0^b	6^a	8	12·0* (3)
17 April–6 June 1980	0	3	0	3	6	—
Total	15^c	89^b	13^c	126^a	243	155·2* (3)

death was not site-related, but was dependent on local weather during each year. Such death was most frequent from December 1978 to February 1979 (Fig. 10); most or all deaths in some cohorts occurred during that interval (e.g. 31 October 1978 cohort at the moist site and the 2 November 1978 cohort at the dry site; Figs 2 & 8). Susceptibility to winter death was not significantly different among cohorts emerging from late summer to winter. Death induced by frost-heaving alone likely occurred whenever air temperatures fluctuated about 0 °C and the ground was bare (e.g. deaths in the third year populations at the moist and mesic sites; Figs 3 & 6, Tables 3 & 6).

Plant death can be attributed to grazing in only four populations and was largely restricted to plants emergent before late winter on the moist and dry sites. Death by grazing (as a percentage of all deaths) was largest for the 2 November 1979 cohort (6·4%) and the

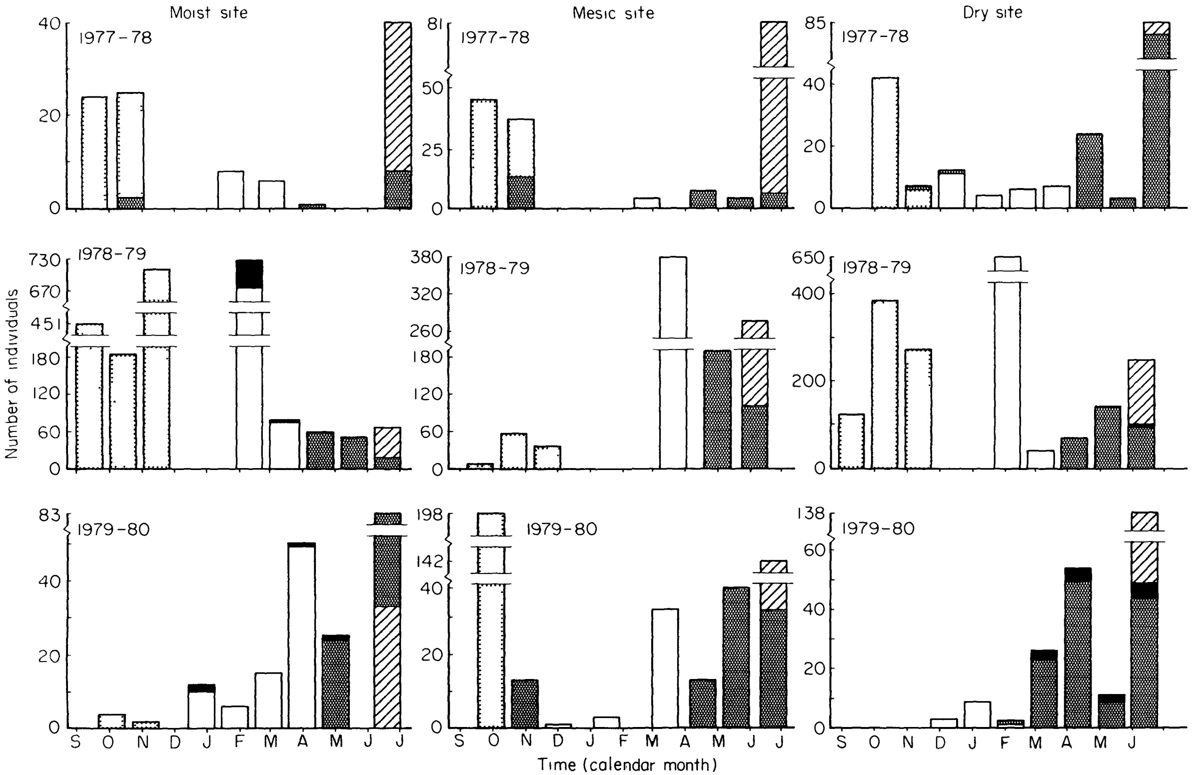

FIG 10. All deaths classified by cause of mortality for *Bromus tectorum* seedlings from late summer 1977 until June 1980. Deaths are totalled for each census date irrespective of cohort for each population at three sites in eastern Washington, U.S.A. Symbols: (⬚), desiccation; (▨), smut; (■), grazing; (□), winter death; (▩), unknown.

7 December 1979 cohort (9·2%) at the dry site (Table 9). Most grazing at the moist site was near the runways of *Microtus montanus* Peale. At the dry site cottontail rabbits (*Sylvilagus nuttallii* Bachman) were the principal grazers; they were frequently seen on the plots. Examination of their faeces suggested that *Bromus tectorum* comprised 67% of their diet. Only two plants, found within the spoor of white-tailed deer (*Odocoileus virginianus* var. *ochrourus* V. Bailey), died from trampling and are included under the grazed category for the 13 November cohort at the moist site (Table 3). Cattle were excluded from all three sites.

The standing crop (g m^{-2}) and density (in parentheses, plants $(0{\cdot}2\ m^2)^{-1}$) of *Bromus tectorum* in June, 1978–80 for equivalent 0·2-m^2 plots at the moist, mesic, and dry sites were: 17·2 (294), 2·72 (88), 0·185 (15); 11·0 (214), 16·3 (475), 3·41 (164); 48·2 (263), 9·87 (402), 20·4 (279), respectively. Both indices of average population performance varied widely from year to year at each site independently of habitat type. Moreover, no relation was found between these values and the pattern of weather from August to the following June.

DISCUSSION

These results illustrate that by relating frequent censuses to environmental events the flux within and the fate of a population may be explained. Alternatively, a synoptic index of population performance (e.g. final density or biomass) as seen here is of limited predictive value.

Recruitment

Caryopses of *Bromus tectorum* join the seed bank throughout the summer, although emergence was not detected in these sites before 23 August. Soil temperatures above 30 °C largely prevent germination during most of summer even when soil moisture is available (Hulbert 1955). Summers in eastern Washington are mostly dry; rain usually resumes by late August or early September. The frequency and amount of rainfall during the rest of September and October are erratic; 30-day droughts are common (Fig. 5). While soil temperature declines in late summer, soil-surface moisture is still insufficient for continuous germination, and the emergence of the grass in late summer and autumn is evidently tied to isolated showers. Yet germination is not confined to saturated soil; germination may exceed 45% even when the soil matric potential is −1·65 MPa (−16·5 bar) (Thill, Schirman & Appleby 1979).

Not only is germination restricted in arid habitats to periods of sporadic rainfall, but often the amount of germination is proportional to the amount of precipitation (Juhren, Went & Phillips 1956; Heady 1958). *Bromus tectorum* may respond similarly (cf., the emergence following rains in September and November at the moist site in 1979; Fig. 3) with recruitment modified by surface roughness and evaporation (Bookman 1983). Aside from the differential emergence of seeds buried at various depths, the circumstances by which a rainfall induces only some seeds to germinate are unclear (Jain 1979). Here, as in other winter annuals (Weiss 1981), a cohort may comprise individuals that lose innate dormancy (Hulbert 1955) in the same interval between autumnal rains. Later-emerging cohorts may germinate from seeds that move to the soil surface with the compaction of litter. Seeds may germinate without contact with the mineral soil (Young, Evans & Kay 1971), but survival beyond several weeks is probably poor.

Emergence within a wide temperature range around 0 °C allows the appearance of cohorts in cool months. Within a laboratory germinator, *B. tectorum* may emerge even when the rooting medium remains near 0 °C, suggesting that frequent emergence during winter is not dependent on prolonged warming periods provided the rooting medium remains saturated with water. Germination is not inhibited even when temperatures diurnally drop briefly below freezing. Thill, Schirman & Appleby (1979) report 70% germination of *B. tectorum* seeds with temperature fluctuating sinusoidally from −2·5 to 12 °C. Insulation by snow may extend emergence into winter. Some emergence was detected within a day after the loss of snow, suggesting that *B. tectorum* may germinate under melting snow (e.g. the 12 February 1979 cohort at the dry site; Fig. 8).

Mortality

Commonly the seedling is the most vulnerable vegetative stage (Harper 1977); for *B. tectorum* most deaths occurred within 60 days after emergence. Desiccation was the principal killer in populations in which early seedling mortality was prominent (Fig. 10). Seedlings with radicles less than 15 mm long (seedlings about 1 day old) will die after 2 weeks of drought (Hulbert 1955). As tabulated here, death by desiccation is underestimated, because no estimates of the death of pre-emergent plants were possible under field conditions. In laboratory trials one day elapses between emergence of the radicle and the epicotyl at room temperature, an interval that probably increases as temperature of the rooting medium declines.

While prolonged snow cover may cause the death of seedlings (Anderson 1947), most winter death was probably caused by frost-heaving, With only sparse litter on these sites (average dry weight of litter in the plots at the moist, mesic, and dry sites in 1981 was 221, 168 and 83 g m^{-2}, respectively), soil-freezing would have begun when the air temperature reached about −1 °C (Anderson 1947). Death coincided most commonly with the rising of peds at the soil surface. Seedlings rooted in these peds and seedlings with roots along the faces of the developing cracks dried out and died. Clusters of seedlings were moved laterally several cm during the unusually severe winter of 1977–78. Biswell *et al.* (1953) found that as many as 88% of the seedling population of the annual *Bromus mollis* L. were heaved by frost on clay and clay-loam soil in California. Both germination and death by frost-heaving in these annual bromes may operate almost simultaneously as temperature fluctuates near 0 °C.

Ustilago bullata is the most conspicuous fungal pest of *Bromus tectorum* in eastern Washington (Fischer 1940). The smut's spores disseminate along with and germinate synchronously with the seeds (Klemmedson & Smith 1964) or later infect the seedling (Hulbert 1955). As seen here, infected plants commonly remain alive, although moribund, until late spring. Perhaps death also occurs among younger plants for the survival of seedlings of *Bromus catharticus* Vahl. can be halved by this smut (Falloon 1979a). Among our sites morbidity by smut is not site-specific but rather depends on each year's weather. Infection by *Ustilago bullata* may occur within a wide range of environmental conditions; Falloon (1979b) found that most seedlings of *Bromus cartharticus* became infected when the soil temperature was less than 30 °C. We did not find any significant difference in morbidity between early autumn and late autumn-emergent plants (*cf.* Hulbert 1955). But Hulbert's (1955) hypothesis that the smut's spores are depleted in the soil through germination in early autumn, may account for the low morbidity among winter and spring-emergent plants (Tables 1, 3, 5, 7 & 9).

Foraging by small mammals has often been identified as an important source of mortality in swards of *B. tectorum* (Piemeisel 1938, 1945). Both *Microtus montanus* and the widely foraging *Peromyscus maniculatus* Wagner commonly reach their highest annual density at the moist site between late autumn and winter (Farris 1971). As a result, both mammals probably caused deaths in winter, especially *Microtus montanus* which is active under the snow. Numerous runways were evident at the moist site as snow melted.

The omnivore *Peromyscus maniculatus* (Jameson 1952) probably relies on vegetative material, including *Bromus tectorum* at the dry site in winter. *Microtus montanus* is uncommon. Assessment of cottontail rabbits as the chief foragers is based in part on the prominence of *Bromus tectorum* in faeces in the plots. These data suggest the importance of *B. tectorum* to rabbits but not necessarily the reverse, although no other herbivores are as prominent about these plots. Non-lethal grazing of *B. tectorum* by insects was observed at all the study sites. At the dry site the grasshoppers *Melanoplus sanguinipes* F. (Rogers & Uresk 1974) and *Ageneotettix deorum* Scudder (Sheldon & Rogers 1978) are minor foragers.

On 18 May 1980 layers of ash from the erupting Mount St Helens, approximately 0·5, 20 and 10 mm thick, were deposited on the dry, mesic, and moist sites, respectively (Sarna-Wojcicki *et al.* 1981). Of the few deaths of *Bromus tectorum* in late May until harvest in June, none could be attributed to the ash. Caryopses of *B. tectorum* filled after 18 May even on sites where the compacted ash was greater than 3 cm thick (Mack 1981b).

For a continually-germinating annual, explanation of a population's fate is dependent on quantifying the environment of each cohort; for example, the environment during recruitment varies substantially between plants emerging in late August and early May. Members of a population differing in age by several weeks may show markedly different responses to mortality agents. Some cohorts of annuals may altogether avoid mortality agents restricted to one season (e.g. frost-heaving, frost injury). The use of dynamic compared with static survivorship curves has long underscored recognition of the different environments experienced among cohorts, although the importance of this distinction for annual plants has emerged only recently (Marks & Prince 1981). Reliance on the average performance of a mixed-age group as a biologically meaningful summary of plant response to environmental change is an often uninformative and an unnecessarily restrictive practice. Furthermore, when environmental measurements and demography are used together detection of cause and effect is improved.

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