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STUDIES ON PLANT DEMOGRAPHY: *RANUNCULUS REPENS* L., *R. BULBOSUS* L. AND *R. ACRIS* L.

I. POPULATION FLUX AND SURVIVORSHIP

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INTRODUCTION

'Every being, which during its natural life time produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product' (Darwin 1859). It is the task of the demographer to describe and attempt to explain numbers and changes in numbers of organisms and most of our present knowledge of the biology of populations has been based upon studies of animals. Very few papers provide even elementary actuarial data about plant populations. The behaviour of a population is dominated by the births, deaths and migrations of its individuals. In plants, birth, that is to say seed production and vegetative multiplication, has been the subject of extensive anecdotal biology and the elegant beginnings of a systematic treatment by Salisbury (1942). Migration has been examined primarily in anecdotal examples and mortality has been particularly neglected. Mortality in some crop and weed populations has been studied in field plot experiments (Harper & Gajic 1961; Harper & McNaughton 1962) and formal analyses of such simple populations have been developed and reviewed by Yoda *et al.* (1963) and White & Harper (1970). However, mortality data from natural populations have rarely been recorded, perhaps partly because it is more difficult to define 'the individual' in plants than it is in animals.

The estimation of annual weed populations and their reproductive potential in a sequence of years can provide the necessary elements to show how plant numbers change from year to year (e.g. *Avena fatua*†, Selman 1970). For other annuals, which are not privileged by agronomic interest, data on population regulation are almost non-existent. A remarkable exception is the study by Sharitz (1970) of two members of a seral community (*Minuartia uniflora* and *Sedum smallii*) in south-eastern United States, where a detailed study of plant numbers was complemented by observations of environmental factors and experimental work on the effects of physical and biotic factors on the regulation of the population.

Although many forestry investigations contain casual information on the mortality of individuals, and, despite the advantage that the age of many trees can easily be determined, no full demographic study appears to have been made on woody perennials. The

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† Nomenclature follows that used in the papers quoted.

most complete plant investigations have been undertaken on perennial herbaceous plants, mostly members of grassland communities.

Tamm (1956) made a study which spanned 14 years, mainly concerned with *Anemone hepatica*, *Centaurea jacea* and *Sanicula europaea* growing in meadow and forest communities. He made yearly observations on his plots, identifying the plants from year to year by their position on a grid and Harper (1967), by rearranging Tamm's data, showed that the mortality risk for the plants present at the start of Tamm's study was so constant that it was reasonable to calculate 'half-life' values for some of the species. It is important that all plants present at the start of the study were grouped, including all ages.

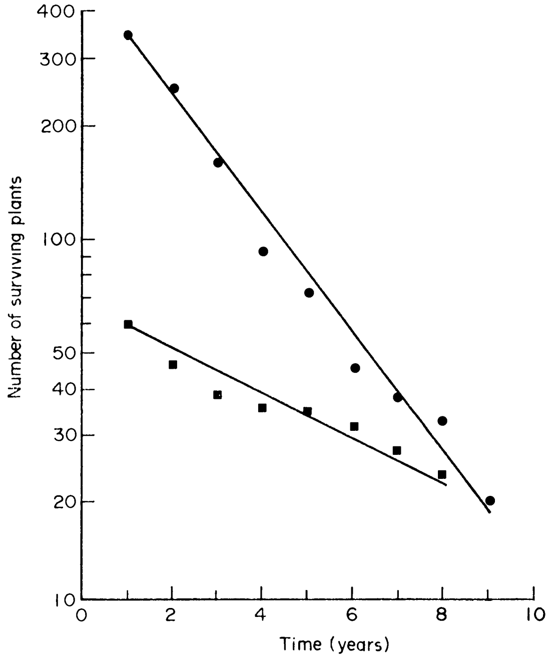

Fig. 1. Survivorship curves for populations of *Ranunculus acris* (●) with a half-life of *c.* 3·0 years and *R. auricomus* (■) with a half-life of *c.* 6·0 years, in meadows of the Oka River (U.S.S.R.). Calculated from data of Rabotnov (1958).

In a similar study of the life cycles of *Ranunculus acris* and *R. auricomus* growing in meadows in the valley of the river Oka in Russia, Rabotnov (1958) observed one 10 m^2 plot for 10 years. The plants were labelled and in this case the behaviour of both the individuals present at the start and that of the new cohorts recruited to the population were recorded. Rabotnov's data have been recalculated and plotted in Fig. 1 to show the number of surviving individuals at each year after the start of the observations. Both populations show a fairly constant rate of mortality, although the rate of death of *R. acris* was considerably higher than that of *R. auricomus*: the half-life of *R. acris* was only 3 years while that of *R. auricomus* was twice as long.

Sagar (1959) made a shorter but more detailed study of field populations of plantains (mainly *Plantago lanceolata*) in permanent grassland in Oxfordshire; he observed and mapped populations with a pantograph and presented the first actuarial analysis in botanical literature. Harper (1967), and later Sagar (1970), discussed part of the data.

The survivorship of the individuals in Sagar's populations is plotted in Fig. 2. Once again, there is a remarkable linearity in the survivorship curve, although there is superimposed a seasonal rhythm with a relatively steeper slope between April and June and a gentler slope in the autumn and winter months. The half-life for the original populations of both 1 m^2 plots was *c.* 13·5 months. Foster (1964), in a short survey of the demography of *Bellis perennis*, observed a slow but very constant mortality process occurring in the populations.

During a genecological study of species tolerant to heavy metals, Antonovics (1966, 1972) observed the longevity of *Anthoxanthum odoratum* growing in the spoils of a mine in Anglesey. He identified individuals by their position along several transects and was able to determine when an individual disappeared from the population and the frequency of recruitment of new ones. Fig. 3 shows the straight survivorship line from two transects (no. 1 and 2) examined by Antonovics.

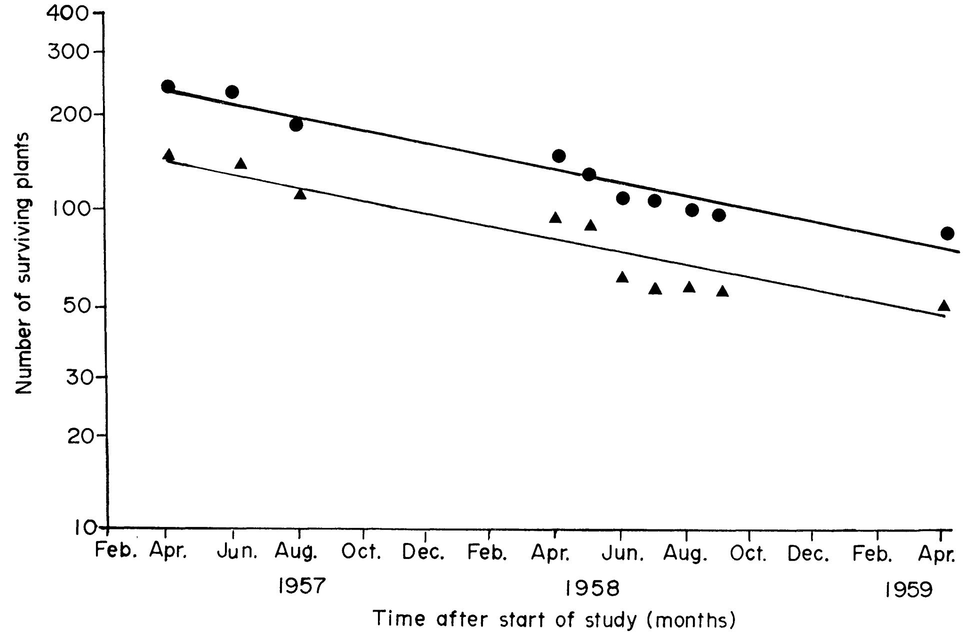

FIG. 2. Survivorship curves for population of *Plantago lanceolata* growing in permanent grassland in Oxfordshire, England. Each site 1 m^2; ●, ▲, replicate sites. Data calculated from Sagar (1959).

In an attempt to evaluate the dependability of range forage grasses, Canfield (1957) used information gathered on a range near Tucson, Arizona, during 17 years of observations in which 'numerous sites on rangelands subject to yearlong grazing' were charted. These sites represent a very wide variety of environmental and management conditions. The charts were mainly obtained using a pantograph, tracing the perimeter of individual grass clumps, each representing an original seedling. About half the plots were enclosed and the rest subject to constant grazing. The species observed were classed as primary or secondary grasses, depending on the degree to which the cattle grazed them.

Fig. 4(a, b) shows the mortality curves of some species of the two groups plotted from Canfield's data. Fig. 4(a) shows that mortality risks of genets* of primary grasses were

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* The term 'genet' is used for the genetic individual (the product of a seed which may be a large clone) distinguished from the ramet, the functional unit in a vegetatively reproducing species.

considerably higher in the grazed than in the protected plots, with the exception of *Trichachne californica*, which increased its half-life from *c*. 4·5 in the ungrazed condition to *c*. 5·0 years in the grazed plots. *Lycurus phleoides* and *Bouteloua hirsuta* both increased their half-life by 1·1 years from grazed to the ungrazed plots (1·6 to 2·7 and 2·1 to 3·2 years, respectively).

The life span of secondary grasses was increased in the grazed situations, the effect of grazing being apparently to reduce interference from the surrounding primary grasses. Nevertheless greater life span did not mean a correspondingly greater half-life: in *B. rothrockii* it increased from 1·5 to 1·6 years, in *B. filiformis* from 1·9 to 2·2 years but in *B. chondrosioides* it remained at 4·5 years.

The most remarkable survivorship curve is that found for species like *Trichachne californica*, *Bouteloua hirsuta* and *B. chondrosioides* in which members of these populations have a relatively riskless middle period of life followed by a more simultaneous time for death than populations of *B. rothrockii* and *B. filiformis* or Tamm's meadow and forest species. This type of negatively skewed curve is typical of human populations and has been observed in other animals such as Dall Mountain sheep and in some populations of birds and rotifers (Deevey 1947), in which although there may be a slightly higher mortality in juvenile forms, a fairly 'safe' stage is reached quickly and maintained for a long period until further increases in age increase the mortality risks sharply.

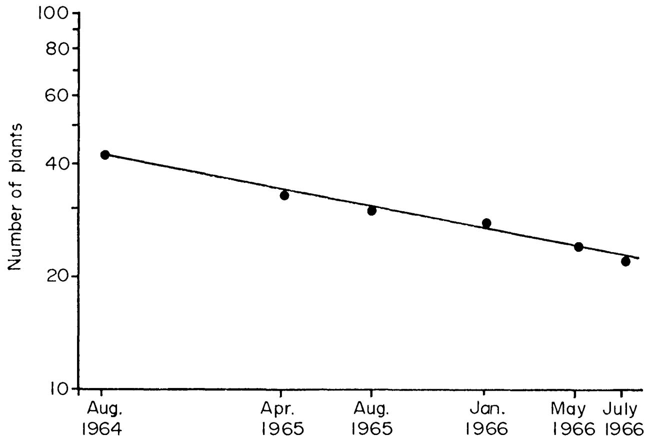

FIG. 3. Survivorship of individuals of *Anthoxanthum odoratum* in a mine spoil population in Anglesey. Data calculated from Antonovics (1966).

More recently Williams (1970) presented data on the survival of two species of semi-desert grassland in Australia, *Danthonia caespitosa* and *Chloris acicularis*. His study covers a long period (16 years) and a large number of plots (324 of 1 m^2), about half of which were protected and half grazed. Observations of the plots were made irregularly and sparsely; there are gaps of up to 4 years between observations. The plants were charted with a pantograph. The data have been pooled from the maps for *Danthonia* and the resulting survivorship curves for three selected 'crops' (populations originated in a given year) are illustrated in Fig. 5. The survivorship curves for protected and grazed populations are quite similar and there is a slight tendency towards a positively skewed survivorship curve, but it is not possible to say if the time lags between observations produce this effect or whether a greater mortality occurred in a particularly unfavourable period. In

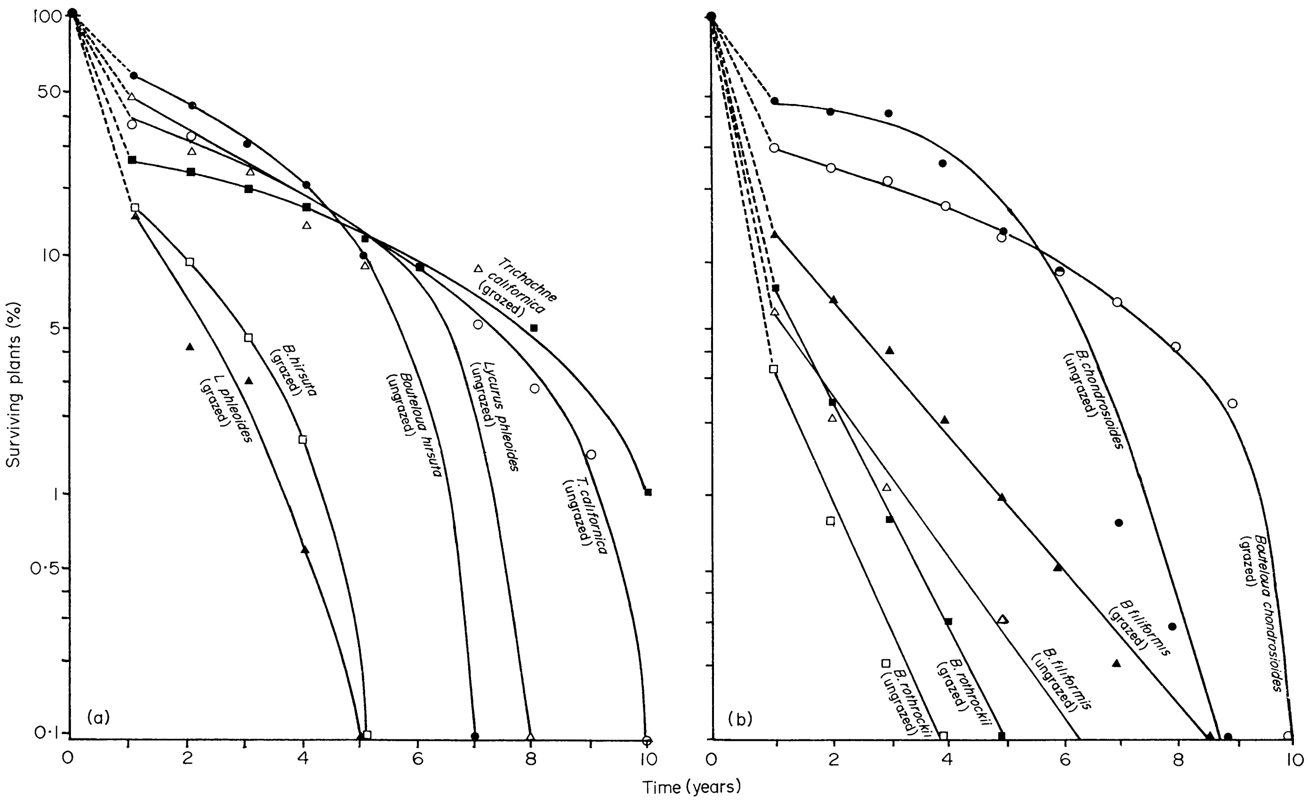

FIG. 4. Survivorship of (a) primary and (b) secondary range grasses in south-eastern Arizona. Drawn from data of Canfield (1957).

this case the survivorship study was made independently on the individual cohorts of recruited seedlings.

From evidence available, it appears that plant populations may present survivorship curves that approximate to the three main types described by Deevey (1947). However, it is significant that all the examples of mature populations whose survivorship curves depart significantly from the exponential type of decay are those obtained from grasses where observations have been widely separated in time. There is a special problem in analysing such data. Grass plants are composed of many tillers or ramets and the tiller, not the clump or genet, may be the appropriate unit to consider in survivorship studies. Certainly, as is shown in a later section of this paper, the ramet rather than the genet of *Ranunculus repens* is the effective unit in population regulation.

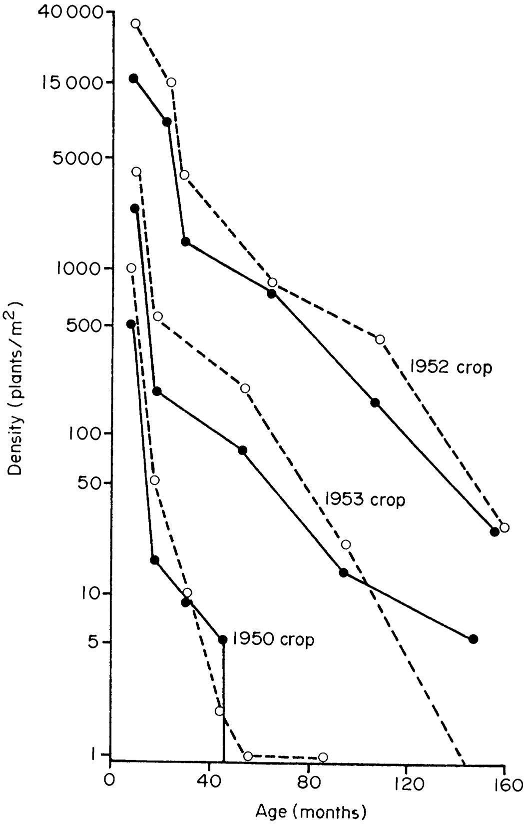

FIG. 5. Survival of clumps of *Danthonia caespitosa* in grazed (○) and protected (●) disclimax grassland for the 1950, 1952 and 1953 crops in semi-arid Australia. Redrawn from Williams (1970).

Hett & Loucks (1971) have shown that their data on mortality in young populations of sugar maple plants fitted either the negative exponential model of Deevey ($y = e^{-bt}$) or the power function model ($y = x^{-bt}$). They observed no significant difference between the goodness of fit of the two models. The fitting of a precise mathematical model to describe mortality in plant populations is perhaps of secondary importance compared with obtaining detailed information on the rates of mortality of populations at such close intervals that it permits the search for, and analysis of, the causes of mortality during the different stages of the life of plants. Then a more appropriate model could be developed and its applicability tested in other situations.

Information about the population flux of plants is very scanty. A few examples show how many plants may be recorded 'passing through' a small area in a short time even without very detailed observations. Records in a 1 m^2 population of *Plantago lanceolata* (Sagar 1970) showed that 1150 plants were observed to appear in only 2 years; Rabotnov (1956, 1958) observed 1150 plants of *Ranunculus acris* in a 10 m^2 site in 10 years and 280 plants of *Heracleum sibiricum* in 20 m^2 during 5 years.

It seems clear, therefore, that it is only with studies where very frequent and detailed observations of the sites are carried out that the size of the cast of plants which take part in the ecological play of a population becomes evident. It is also essential to observe the performance of the individuals in terms of size and reproductive output in order to reveal those effects of biotic and physical factors which are otherwise disguised by simply considering numbers.

The aims of this study of the populations of three buttercup species were: (a) to make detailed observations on the demography of field populations in which the fate of individuals could be followed and accurate information on population flux and mortality rates at short intervals obtained; (b) to record the reproductive performance of each individual under different environmental conditions in order to know the degree of reliance of the species on seed and vegetative reproduction and their reproductive potential; (c) to investigate the energetic pathways followed by the three species in their vegetative and reproductive strategies; and (d) to explore and compare by means of population models the adaptive significance of the life strategies of the three species (i.e. their rates of reproduction and mortality, the efficiencies of their modes of reproduction and their energetic costs).

The present paper is concerned with the analysis of population flux and the mortality processes that operate on the populations of the three selected species of *Ranunculus*.

MATERIALS AND METHODS

The species studied

The ideal species for comparative demographic studies should be (1) closely related, (2) very common, (3) living in the same area within an extensive and stable ecosystem, and (4) representative of contrasting life-cycle strategies. Furthermore they should produce (i) well-defined, discrete vegetative propagules which are connected by above-ground structures, readily distinguishable from the parent plant and other propagules and quickly become independent of the parent, (ii) conspicuous seeds which are not subject to extensive migration and which present no serious dormancy problems, (iii) seedlings and vegetative propagules at discrete periods in the year, and (iv) adult plant bodies with markedly different phenology and some morphological character that permits the age of the plants to be determined.

This ideal cannot be realized but the three buttercups (*Ranunculus repens*, *R. bulbosus*, *R. acris*) possess most of the 'ideal' characteristics. All three species are extremely common and of very wide distribution and belong to one section (Chrysanthe) of the genus. They often occur together in grasslands in Britain; a detailed account of their biology was given by Harper (1957) and is summarized in Table 1.

The grassland community in which the three buttercups cohabit has been created by man. They are rarely found together in 'natural' vegetation in Britain and it is unclear what were their natural habitats in Britain prior to man's activities though it has been suggested (Harper 1958) that *R. repens* might have been a species of damp woodland, marshes and a component of the vegetation of the oldest parts of dune slacks (where it occurs in present times), *R. bulbosus* of seral stages on thin, well-drained, calcareous soils and *R. acris* of a variety of communities from marshes and fens to mountain grasslands.

Subtle differences in ecological requirements determine the areas occupied by the three species in the field. Perhaps their clearest ecological separation occurs in the 'ridge and furrow' grasslands established on former arable lands (Harper & Sagar 1953); here *R. repens* occupies the bottom of the furrow which is poorly drained and often waterlogged, *R. bulbosus* grows along the ridges where drainage is more effective, and *R. acris* occupies an intermediate position. Microtopographical differences in 'flat' grasslands produce the same zonal distribution. One factor responsible for this zonation is a difference in the requirements for germination and survival of seedlings. *R. repens* is very successful in establishing under waterlogged conditions, *R. bulbosus* in freely drained soils and *R. acris* in intermediate conditions (Harper & Sagar 1953).

Table 1. *Comparison of characters of the three species of buttercup* (Ranunculus)

	R. repens	*R. bulbosus*	*R. acris*
Type of stem	Short vertical rhizome	Corm	Short vertical or oblique rhizome
State in winter	As a rosette	As a rosette	As a rosette
Summer rest	None	From July to September	None
Reproduction	Mostly vegetative, some seed	Exclusively seed	Mostly seed, some vegetative
Flowering peak	End of June	End of May	Late June to mid-July
Germination	Late April to late July	Late September to mid-November	Late May
Physiologic renewal	Large proportion of adults replaced by new vegetative units in late summer	All adults renew their tissues in the winter and spring	Only leaves renewed

Despite their taxonomic affinities, cohabitation, overlapping of flowering seasons and indiscriminate pollinators, no definite evidence of natural hybrids exists and attempts to produce these artificially have failed.

The three species have specialized stems; *R. repens* and *R. acris* possess short, stout rhizomes which store some food reserves. *R. bulbosus* has a corm which serves for food storage and as a summer perennating organ. The presence of the highly unpalatable and toxic glucoside ranunculin in plants of *R. bulbosus* and *R. acris*, especially the former, causes cattle to avoid grazing plants of these species and their immediate neighbours. *R. repens* has a considerably lower content of ranunculin and is grazed with little discrimination.

The achenes of the three species are disc-shaped, *c.* 3 mm in diameter and are readily distinguished from the seeds of other grassland species. It is, however, difficult to distinguish between achenes of the three species of *Ranunculus* after they have been shed.

R. repens

Plants overwinter as rosettes, 2–3 cm in diameter, with two to four leaves. In spring *R. repens* starts forming new leaves on longer petioles around a short stem. By the end of May, it begins to produce epigeal stolons which arise at angles of *c.* $x \times 60°$ of the first to be formed. Usually one or two stolons are produced by each plant, although some plants can form up to five primary stolons which in turn may branch and produce secondaries; further branching is very infrequent in grassland where maximum stolon lengths rarely if ever exceed 50 cm. There are usually three or four internodes of variable length in each stolon, the shortest (3–4 mm) normally being produced immediately next to the parent plant; internodes up to 15 cm long may be produced, but the most frequent internode length is *c.* 5 cm. The patterns of branching and internode length are of course the critical determinants of the distribution pattern of vegetative daughters. The nodes bear one or two leaves and a pair of root initials that grow downwards anchoring the stolon to the ground. The production and growth of stolons reach a maximum by mid-July and can extend well into October during mild, humid weather.

Once a node has rooted successfully, additional leaves and roots are produced. By the end of August the stolons connecting the daughter plants to the parent start to wither. Biting and trampling by live-stock accelerate the rate at which the vegetative propagules become independent and most plants achieve complete separation by mid-September. A large proportion of the parent plants die after vegetative reproduction. At this time the newly established daughters have three to five small leaves and are in all respects similar to the surviving older plants: the whole population then begins the change to the winter rosette habit.

Flowers are normally produced solitarily at the nodes on short stalks (usually less than 10 cm long). Flowering reaches its peak at the end of June but isolated plants can flower as late as October.

R. bulbosus

This species becomes active during the late winter when it begins to mobilize the reserves in its corm to produce a few additional leaves to the rosette and starts to form a new corm; the old corm dies and by mid-May has usually disappeared completely: there is no perennial part. During late April and May the plants expand new and larger leaves and produce a flower stalk *c.* 30 cm high bearing 8–15 flowers. These characters show considerable plasticity; Salisbury (1942) observed that seed output per plant can vary ten-fold from 69 when plants were under 'severe competition' to 687 when they were subjected to 'no competition'. Flowering reaches a peak by the end of May and fruits can still be found on the stalks at the end of June and mid-July. By this time all the aerial parts of the plant have withered leaving a small hole in the ground through which the corm is often visible. The plant then enters a period of aestivation which coincides with the driest part of the summer. With the arrival of the late summer and autumn rains, a lateral bud gives rise to a new rosette, which develops a new corm early in the next year. It is very rare for a parent corm to produce more than one replacement in a given year.

R. acris

With the onset of warmer temperatures in early spring, the overwintered rosette of *R. acris* begins to develop new and bigger leaves. Leaf production is relatively precocious but the flowering peak is later than that of the other species (late June and early July) and many plants continue flowering until late September. *R. acris* produces the tallest flower stalks (usually 40–60 cm) and the largest number of flowers per plant of the three species. Seed can still be found on the plants in unmown grasslands up to the beginning of October. All the mature leaves and the flower stalks decay and are replaced by the over-wintering rosette. Vegetative reproduction occurs in the autumn but only sparsely; a small branch of the rhizome produces a new vegetative plant only a few millimetres from the parent. The new plants become well established by the following spring and, as the rhizomatous connection slowly decays, they separate from the parents, forming over the years a very tightly clumped colony of usually three to six plants. The three species therefore differ sharply in their ability to reproduce vegetatively and in the spacing pattern of the products.

The field

A field of *c.* 1 ha of coastal grassland was selected at Henfaes, College Farm, Aber, Caerns. (Nat. Grid Ref. SH 653733). This field had been under continuous traditional sheep and cattle grazing for at least 50 years. During this period it had not been ploughed nor had it received any herbicidal treatment. Fig. 6 shows the management of the field during the period of the study. Sheep grazing takes place chiefly from late autumn to the spring, the field is normally grazed by cattle between the sheep-grazing periods and a few horses are regularly kept in the field during the late summer. Thistle cutting and manuring were done regularly between August and September every year, except in 1970. A deviation from normal grazing practice (over-stocking in the wet winter of 1969–70) resulted in heavy poaching* and caused serious damage to certain areas of the field.

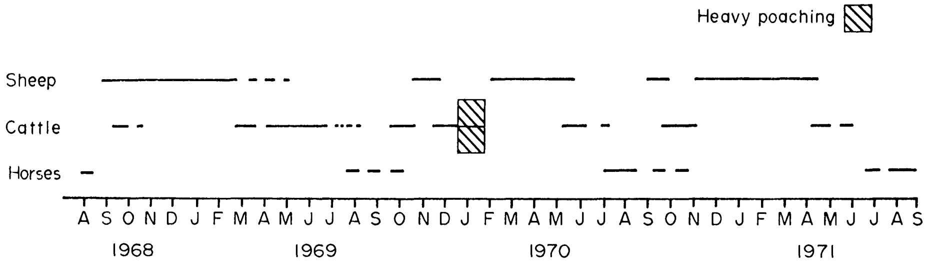

FIG. 6. Summary of grazing activities in the experimental field at Henfaes, College Farm, Aber, during the period covered by the study.

The field had a very gentle slope and a depression that divided it diagonally. Associated with the differences in drainage a wide range of population densities of the three buttercups occurred.

The sward included *c.* 50 species of flowering plant. *Lolium perenne* was the most abundant: *Agrostis stolonifera* and *A. tenuis*, *Cynosurus cristatus*, *Festuca rubra*, *Holcus lanatus*, *Poa annua* and *P. trivialis* were also common. Of the dicotyledonous species *Trifolium repens* was by far the most abundant; *Achillea millefolium*, *Bellis perennis*, *Leontodon autumnalis*, *Plantago lanceolata*, *P. major* and *Rumex acetosa* were very common; *Cirsium arvense* formed dense patches in isolated areas in the field.

Voles were seen active in early spring and there was evidence of mole activity toward the margins of the field; groups of different bird species visited the field for long periods during late winter and early spring.

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* Poaching—damage to soil and vegetation by trampling, particularly by hooves on waterlogged soil.

Table 2. *Summary of climatic data for the period* 1969–1971

	Temperature (°C) Mean min.	Temperature (°C) Mean max.	Rainfall (mm)
October 1969 to March 1970	4·1	9·6	622
October 1970 to March 1971	4·9	10·1	690
April to September 1969	9·6	16·6	349
April to September 1970	10·1	16·3	445

The climate

Climatic data for an 8-year period, including the 3 years covered by the study, were obtained from the College Farm Meteorological Station at Aber and are presented in Fig. 7. The summary of the climatic data for the period 1969–71 in Table 2 shows that the growing season of 1970 was wetter and milder, with less thermic variation, than the 1969 growing season; similarly, the period October 1970 to March 1971 was milder, wetter and with narrower thermic variation than the same period between 1969 and 1970.

Sites and recording techniques

A number of methods can be used for studying the population dynamics of plants in field conditions but in grassland systems, where grazing activities have to be kept unchanged, the possibilities are greatly reduced. The canopy density, the complex composition of old swards and the activities of grazing animals rule out such methods as photographic recording or labelling of individuals; even the location of the permanent sites has to be made in such a way that the grazing behaviour of the animals is not affected.

The permanent sites were chosen subjectively. An attempt was made to include a convenient range of population densities of the three species, as well as a variety of different drainage conditions (see Table 3). Seven groups of three 1 m^2 sites were chosen

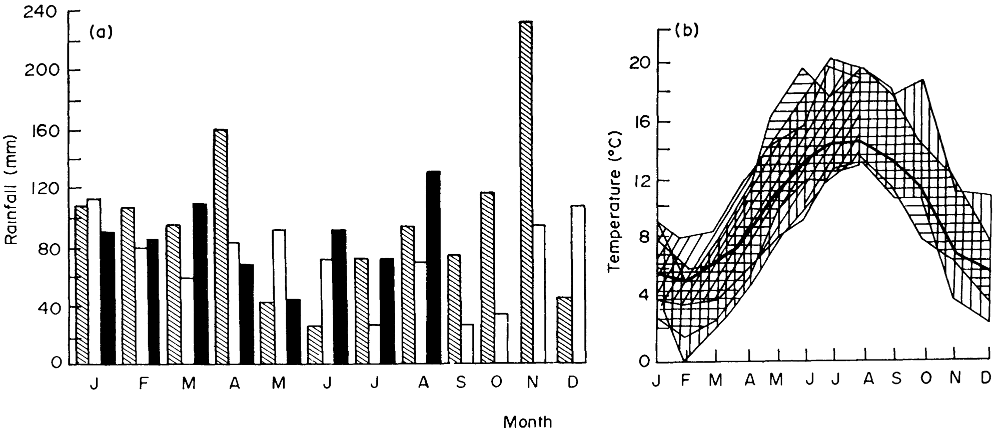


FIG. 7. (a) Rainfall distribution for the period covered by the study. Hatched columns, 1969; open columns, 1970; filled columns, 1971 (data of 1971 until August only). (b) Monthly mean maximum and minimum temperatures during the period covered by the study and average monthly temperature for the period 1964–68. Data for 1971 until August only. Average, heavy continuous line; 1969, vertical hatching; 1970, horizontal hatching; 1971, diagonal hatching.

(21 × 1 m^2). Each group of three 1 m^2 plots was located by means of a triangular aluminium frame with sides 5 m long (see Plate 1) which was fixed on to metallic rods sunk into concrete cylinders buried in the ground at the corners of the triangle. Within each triangle three 1 m^2 grids were fixed (two at the base of the triangle, one towards the apex) to aid the mapping operation leaving nothing protruding above the ground that could attract or repel the grazing animals.

Following Sagar's example (1959), a pantograph was adapted to produce maps on tracing paper at a scale of 1:5 of the positions of all the buttercups present at each sampling date at each site. Consecutive maps were superimposed to identify new recruits and plants which had died between observations. This procedure permits accurate recognition of individuals at successive dates at distances apart of 2 mm. Each plant was assigned a number and a punched card on which its behaviour was entered; these observations included the date of its first record, whether the plant originated from a seed or a vegetative propagule, the number of flowers and seeds, stolons, internodes and rooted nodes produced and, eventually, the date of its death.

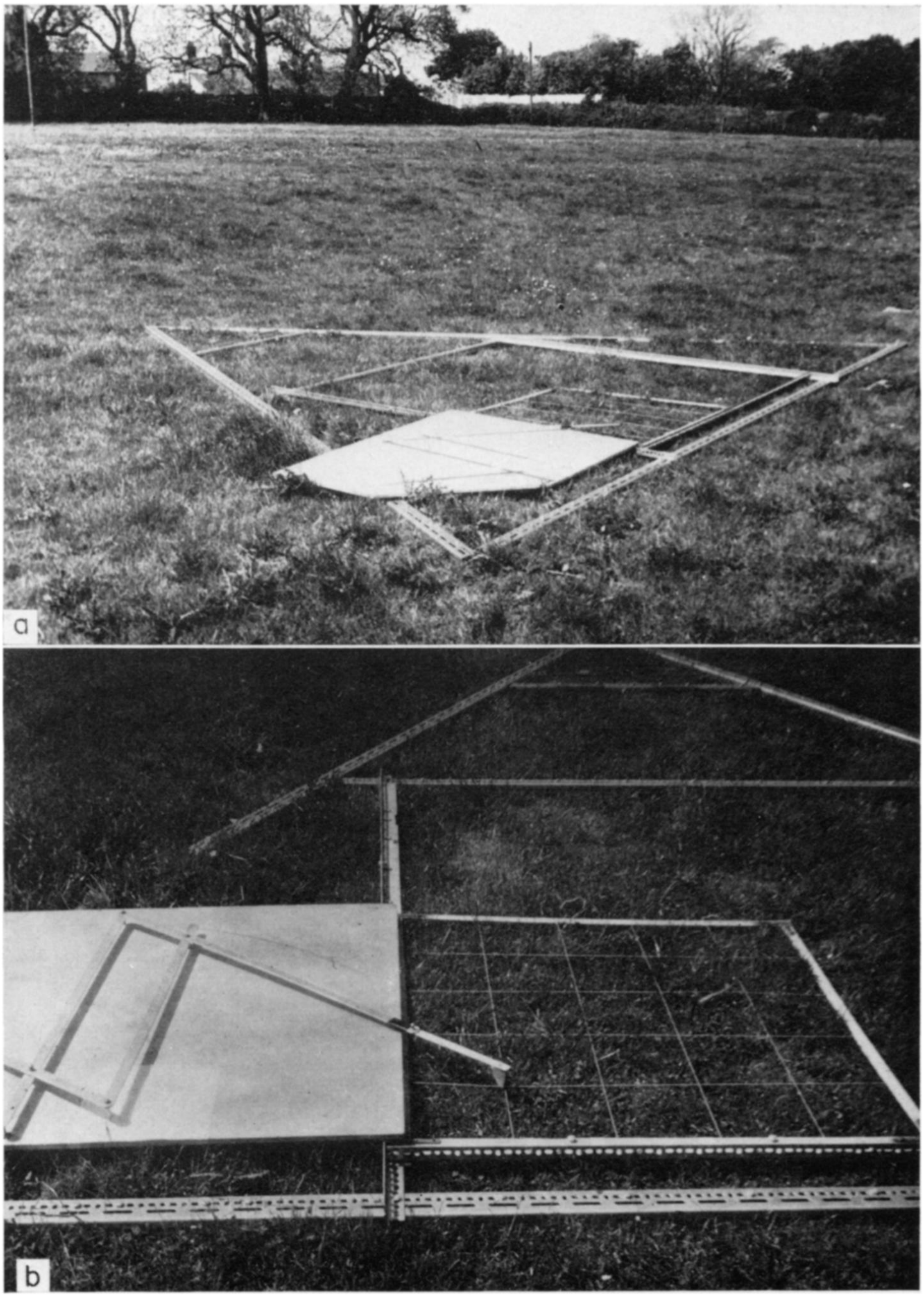
Table 3. *List of sites and their characteristics*

Site	Most abundant buttercup	Density	Drainage	Grazing
A1, A2	*Ranunculus repens*	High	Moderate	Intense
A3, B1	*R. repens*	Medium	Moderate	Intense
B2	*R. repens*	Low	Moderate	Intense
B3	*R. bulbosus*	High	Good	Intense
C1, C2	*R. repens*	High	Poor	Light
C3	*R. repens*	Low	Poor	Light
D1, D2	*R. acris*	High	Good	Light
D3	*R. acris*	Medium	Good	Light
E1, E2, E3	*R. bulbosus*	Low–medium	Good	Intense
F1, F2, F3	*R. bulbosus*	Low–medium	Good	Moderate
G1, G2, G3	*R. bulbosus*	Medium–high	Good	Light

Observations were started in March 1969 and made at intervals which were dictated mainly by the stage of growth of the populations. From March to October observations were usually made every 15 days, the time required to complete a round of mappings of all 21 m^2. Mapping was done most frequently for *Ranunculus repens* and *R. acris* during June–August because of the death of the aerial organs of *R. bulbosus* and the most frequent sampling of this species was from September to November when germination occurs; the similar intensive study of *R. acris* and *R. repens* was made between March and May during their respective germination periods. Observations were made monthly from December to February, except in the sites that suffered badly from trampling during the 1969–70 winter.

RESULTS AND DISCUSSION

Actuarial information about animal populations is usually presented in the form of life tables for cohorts of a population or for populations with non-overlapping generations (e.g. Deevey 1947; Birch 1948), and normally takes into consideration only their reproductive (female) portion. Actuarial data of populations of perennial plants cannot be treated in this fashion except when the behaviour of particular cohorts or 'crops' is being considered.



(a) General view of the field at Aber, Caerns., and the portable aluminium frame used to relocate the permanent sites. (b) Pantograph used for the mapping of plants. The 1 m^2 grid delimited each permanent site and helped in a systematic census of the plants. Photographs by W. Neville.

Table 4. *Population flux in* Ranunculus repens *sites* (*each site* 1 m^2)

		A1	A2	A3	B1	B2	C1	C2	C3
(a)	No. of plants/m^2, April 1969	385	283	201	117	38	148	199	60
(b)	No. of plants/m^2, April 1971	157	155	126	139	63	222	246	87
(c)	Net change (b−a)	−228	−128	−75	+22	+25	+74	+47	+27
(d)	Rate of increase (b/a)	0·41	0·55	0·63	1·19	1·66	1·50	1·24	1·45
(e)	No. of plants arrived between April 1969 and April 1971	344	288	257	244	138	466	499	128
(f)	Total no. of plants lost between April 1969 and April 1971	577	416	332	222	113	390	458	101
(g)	Plants present April 1969, alive by April 1971	25	25	12	13	3	11	12	8
(h)	Percentage survival of plants in (a) (g/a × 100)	6·5	8·8	6·0	11·1	7·9	7·4	6·0	13·3
(i)	Expected time for complete turnover (years) $\left(\frac{2}{100-h}\times 100\right)$	2·14	2·19	2·13	2·25	2·17	2·16	2·13	2·31
(j)	Total plants recorded during study	729	571	458	361	176	612	698	188
(k)	Percentage annual mortality of all individuals $\left(\frac{f}{j}\times 100\right)$	79·1	72·8	72·5	61·5	64·2	63·7	65·6	53·7

Table 5. *Population flux in* Ranunculus bulbosus *sites* (*each site* 1 m^2)

		B3	E1	E2	E3	F1	F2	F3	G1	G2	G3
(a)	No. of plants/m^2, April 1969	101	40	65	41	28	21	65	90	50	47
(b)	No. of plants/m^2, April 1971	72	36	39	44	89	139	32	64	193	120
(c)	Net change (b−a)	−29	−4	−26	+3	+61	+118	−33	−26	+143	+73
(d)	Rate of increase (b/a)	0·71	0·90	0·60	1·07	3·18	6·62	0·49	0·71	3·86	2·55
(e)	No. of plants arrived between April 1969 and April 1971	162	37	42	72	171	362	44	84	354	181
(f)	Total no. of plants lost between April 1969 and April 1971	191	41	68	69	110	244	77	110	211	108
(g)	Plants present April 1969, alive by April 1971	42	15	19	7	10	1	18	41	40	28
(h)	Percentage survival of plants in (a) (g/a × 100)	41·6	37·5	29·2	17·1	35·7	4·8	27·7	45·5	80·0	59·6
(i)	Expected time for complete turnover (years) $\left(\frac{2}{100\text{-}h}\times 100\right)$	3·4	3·2	2·8	2·4	3·1	2·1	2·8	3·7	10·0	4·9
(j)	Total plants recorded during study	263	77	107	113	199	383	109	174	404	228
(k)	Percentage annual mortality of all individuals $\left(\frac{f}{j}\times 100\right)$	72·6	53·2	63·5	61·1	55·3	63·7	70·6	63·2	52·2	47·2

Table 6. *Population flux in* Ranunculus acris *sites* (*each site* 1 m^2)

	D2	D3	A2	G2	B3
(a) No. of plants/m^2, April 1969	143	62	28	26	13
(b) No. of plants/m^2, April 1971	275	124	18	15	1
(c) Net change (b−a)	+132	+62	−10	−11	−12
(d) Rate of increase (b/a)	1·92	2·01	0·64	0·57	0·08
(e) No. of plants arrived between April 1969 and April 1971	237	457	56	99	79
(f) Total no. of plants lost between April 1969 and April 1971	1105	395	66	110	91
(g) Plants present April 1969, alive by April 1971	76	33	14	4	–
(h) Percentage survival of plants in (a) (g/a × 100)	53·1	53·2	50·0	15·4	–
(i) Expected time for complete turnover (years) $\left(\frac{2}{100-h} \times 100\right)$	4·3	4·3	4·0	2·4	0·4*
(j) Total plants recorded during study	1380	519	84	125	92
(k) Percentage annual mortality of all individuals $\left(\frac{f}{j} \times 100\right)$	80·0	76·1	78·6	88·0	99·0

* Average time taken by each of the four crops of plants to die (see text).

A summary of the population flux on all the sites is presented in Tables 4, 5 and 6 for *Ranunculus repens*, *R. bulbosus* and *R. acris* respectively. In these tables (a) and (b) refer to the total population (mature plants and seedlings) of the species. Although observations later than April 1971 have been made, a 2-year cycle only is considered here for convenience. Tables 7, 8 and 9 present data about the fates of those plants present when the study started in April 1969.

In a consideration of the various aspects of population dynamics each species is first reviewed separately.

R. repens

Population flux

R. repens was present in eight 1 m^2 sites in which its density varied ten-fold (38/m^2 in site B2, 385/m^2 in site A1) and averaged *c.* 180 plants/m^2. The net changes in population size were strikingly different in high and low density sites. By the end of the study there was only a four-fold difference between the highest and lowest densities and the average density of all sites had fallen to 150/m^2.

Population densities declined in three sites (A1, A2, A3) due in part to the heavy poaching that affected parts of the field during the 1969–70 winter. The cutting and churning action of the cows' hooves considerably reduced the chances of the newly established vegetative propagules surviving the winter. Sites B1 and B2 were affected by trampling to a lesser degree and soon increased their numbers. Sites C1, C2 and C3—not affected by trampling—showed small but steady increases during the 2-year period.

Fig. 8 shows the changes in net population sizes with time and the cumulative gains and losses that determine them. The fluctuations in population density at each site were remarkably small when compared with the number of plants which were recruited and lost from the population. There was a sequence of gain-dominated and loss-dominated periods during the history of the populations, but losses and gains were not strictly proportional. Despite the wide differences between the original population sizes and in the net changes after 2 years shown at all sites, the percentage survivorship of plants *from the original population* was remarkably constant. The *calculated* time necessary for a complete turnover (i.e. the total disappearance of the members of an even-aged population) varied very little—from 2·1 to 2·3 years. It must be noticed, however, that this figure is derived from the original population recorded in April 1969 and since most of these plants had been produced vegetatively in the summer of 1968, the real turnover time must be nearer to 2·7–2·9 years. This means that the plants of these populations should all have become extinct between the end of May and August 1971. In fact, at the last observation obtained at the beginning of August (cf. Table 9) one site had lost all members of the original population, six sites had between one and six and the last had fifteen remaining plants. It is expected that most of this remnant of the original population would have perished by the end of the period of vegetative reproduction.*

Table 7. *Survivorship data of the April* 1969 *populations of* Ranunculus repens *in the permanent sites of* 1 m^2

		Sites									
		A1	A2	A3		B1	B2		C1	C2	C3
Date	T				T			T			
April 1969	0	385	283	201	0	117	38	0	148	199	60
	2	370	283	195	3	116	38	3	138	188	56
	4	356	268	190	5	111	36	6	122	183	47
	6	335	258	180	9	109	34	9	111	159	45
	9	308	240	168	10	104	31	10	104	139	42
	11	296	227	155	12	102	28	12	93	121	39
	13	272	211	136	14	98	25	15	89	113	35
	16	234	176	123	17	97	23	17	76	94	33
	27	153	108	68	28	77	18	33	37	42	19
April 1970	54	89	64	25	30	70	17	42	31	40	17
	56	88	63	25	32	56	17	50	27	40	16
	58	75	61	23	55	27	9	51	27	40	16
	60	67	59	21	57	27	9	56	27	37	15
	62	58	49	19	59	26	9	57	27	36	15
	66	49	46	19	61	25	9	59	22	33	14
	68	40	43	18	65	23	9	62	20	30	14
	73	28	36	15	67	23	8	65	19	27	14
	77	27	30	14	69	19	6	68	18	27	13
	81	25	26	13	75	15	4	69	18	25	13
April 1971	105	25	25	12	78	13	3	71	18	20	10
	115	18	17	11	106	13	3	82	11	12	8
	119	18	6	9	118	10	3	107	11	12	8
August 1971	122	15	3	6	121	8	3	118	9	9	5
					123	0	1	122	4	7	5

T = weeks after initiation of study.

The percentage annual mortality of all individuals present in the population also shows only narrow variation, perhaps with the exception of site C3 (see Table 4).

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* Note added by I. Soane, November 1972. In fact *c.* 60% of this remnant had died by the end of 1971 and by September 1972 only two of the original plants remained. These long-lived individuals had contributed little to the vegetative reproduction of the population in 1971. Only one plant attained average stolon growth, three produced one very short one-noded stolon and the remainder did not show any stolon growth.

Age structure of the living population

Two years of observations are not usually enough to obtain a precise picture of the age structure of populations of perennial plants. In the case of *R. repens*, however, in which most of the original plants have been renewed by the second year, it is possible to determine the age distribution of the living population at the end of the study as well as the ages attained at death. In the case of *R. repens*, the age of the organism refers mostly to the age of the ramet and not to the age of the genet. It would be necessary to follow the fate of individual clones for a considerable period of time in order to assess the longevity of genets.

Table 8. *Survivorship data of the April* 1969 *populations of* Ranunculus bulbosus *in the permanent sites of* 1 *m*^{2}

	Sites													
		B3		E1	E2	E3		F1	F2	F3		G1	G2	G3
Date	T		T				T				T			
April 1969	0	101	0	40	65	41	0	28	21	65	0	90	50	47
	4	100	5	38	65	40	5	28	20	63	4	88	50	47
	5	96	6	38	62	38	6	27	20	55	5	86	50	47
	9	91	8	36	60	34	8	23	17	53	8	81	50	47
	10	88	11	36	56	31	11	23	15	51	10	76	49	43
	12	80	13	34	50	28	18	22	14	45	13	75	48	40
	14	74	26	32	38	28	27	20	10	35	15	70	43	37
	17	71	29	32	37	25	28	20	10	34	23	70	42	37
	28	65	30	32	36	24	30	19	10	28	26	70	42	37
	30	63	31	30	36	24	31	17	10	28	28	70	42	37
	32	63	56	20	23	9	57	11	2	20	32	70	42	36
April 1970	55	54	58	18	23	8	58	11	1	20	42	69	42	36
	57	52	60	18	23	8	60	11	1	20	50	69	41	36
	59	52	62	17	21	8	62	11	1	20	54	67	41	36
	61	50	67	16	20	8	66	11	1	20	56	66	41	36
	65	49	77	16	20	8	77	11	1	20	58	64	41	36
	76	49	82	16	20	8	78	11	1	20	59	61	41	35
	78	48	106	15	19	7	82	11	1	20	62	55	41	35
April 1971	107	42					107	10	1	18	66	52	41	33
											77	50	41	33
											81	50	41	33
											107	41	40	28

T = weeks after initiation of study.

Table 10 and Fig. 9 show the age distribution of the eight populations of *R. repens*. Plants have been categorized according to their year of birth.* There is a normal age distribution with greater representation of younger age-classes except in those sites (e.g. A1, A2 and B1) that were most trampled in the winter of 1969–70. In these sites, the category of plants born prior to the commencement of the study in 1968 is equally or better represented than that of plants born in 1969. The well-established plants formed in 1968, and perhaps earlier, survived the trampling better than the ramets which had been produced some 3 months before the disturbance.

The lightly grazed sites (C1, C2, C3), even early in the germinating season, carried a larger number of seedling recruits in 1971 than the more intensely grazed sites. However,

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* The term 'birth' is here used for plants to indicate the recruitment of plants to the population, whether these plants are genets or ramets—see footnote to p. 677.

established seedlings appear to live longer on the severely grazed sites. No seedlings born in 1969 survived to April 1971 in the lightly grazed sites.

The pattern of distribution of plants in the various age categories changes abruptly after the summer, provided no catastrophic events occur. The class of plants born in 1971 became better represented as plants in the older categories died.

Table 9. *Survivorship data of the April* 1969 *populations of* Ranunculus acris *in the permanent sites of* 1 *m*^{2}

						Sites								
		D2		D3			A2		G2		B3			
Date	T	M	S	M	S	T	M	T	M	T	M			
April 1969	0	143	257	62	126	0	28	0	26	0	13			
	3	143	133	56	76	2	28	4	23	4	9			
	6	129	97	52	60	4	28	5	23	5	9			
	9	123	68	51	52	6	28	8	23	9	3	M		
	11	112	56	48	38	9	27	10	23	10	0	22		
	13	102	48	42	27	11	27	13	23	12		8		
	15	102	44	40	25	13	27	15	21	14		4		
	18	97	39	39	23	16	26	23	20	17		3		
	33	85	35	38	19	27	20	26	17	28		1		
	43	84	32	38	18	54	18	28	17	30		1		
	50	81	31	38	17	56	17	32	16	32		1	S	
April 1970	52	81	29	36	17	58	17	42	15	55		0	12	
	53	81	27	36	17	60	16	50	15	57			6	M
	56	79	27	36	15	62	16	54	15	59			0	3
	58	79	26	36	14	66	16	56	13	61				2
	62	78	24	33	14	68	16	58	12	65				1
	68	75	20	33	14	73	16	59	11	76				1
	75	68	19	30	14	77	16	62	11	78				1
	100	65	19	28	12	81	15	66	8	107				1
April 1971	107	61	11	22	12	105	14	77	5					
								81	5					
								107	4					

T = time (in weeks) after initiation of study; M = mature population;
S = seedlings emerged at T = 0.

The age distribution before the onset of the growing season was very constant in the undisturbed sites. About 70% of the population was 1-year-old plants, 20% of 2-year-olds, and *c.* 5% of older plants (of which a majority should be 3-year-old plants, judging from the calculated time for turnover). The remainder consisted of newly emerged seedlings.

Age distribution of dead plants

Owing to the high turnover rate, the number of plants that were born and died within the duration of the study is large, indeed greater than the whole living population at the end of the 2-year period. Table 11 and Fig. 10 show the number of plants distributed between the five age-classes, 0–0·5, 0·6–1·0, 1·1–1·5, 1·6–2·0 and 2·1–2·5 years.

Of all the plants that died during the study, 70% had arisen as ramets. Plants originating from seed accounted for *c.* 65% of the early mortality (0–0·5 years) while 95% of the plants dying at age 0·5–1 year were ramets. Very few plants produced from seed lived for more than 1·5 years. Only one seedling from all sites died having attained an age of more than 2 years.

Ramets suffered their greatest mortality at ages 0·5–1 year and 1·5–2 years. These ages correspond to the first and second occasion in which the plants passed through the

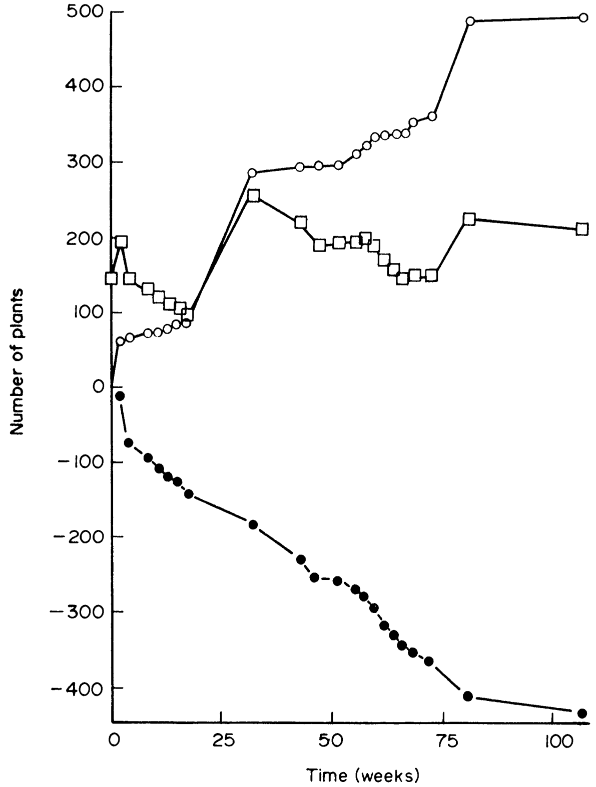

FIG. 8. Changes in population size of *Ranunculus repens* (plants/m^2) at site C1. ○, Cumulative gains; ●, cumulative losses; □, net population size.

Table 10. *Age structure of the living populations of* Ranunculus repens *at the end of the study, April* 1971 (*figures under each age category are percentages of the total populations*)

Site	Year when plants were born				
	1971	1970	1969	Prior	Total
A1	0·6	74·0	10·2	15·8	158
A2	0·6	66·0	17·0	16·3	153
A3	0·0	65·9	24·6	9·5	126
B1	0·0	79·0	11·5	9·3	139
B2	0·0	73·1	22·2	4·7	63
C1	2·2	69·8	22·8	4·9	222
C2	0·8	65·4	28·8	5·0	240
C3	9·2	51·7	29·9	9·2	87

growing period of spring and summer; mortality in the autumn and winter months (when most plants are either less than 0·5 or between 1·0 and 1·5 years old) is comparatively slight. This alternation of high and low periods of mortality contrasts with the rather normal distribution of ages in the populations of dead plants originated from seed (cf. Fig. 10). In these figures there is likely to be some under-representation of the older categories since the chance of recording the death of short-lived plants in a 2·5-year period is greater than that of recording long-lived plants. A longer period of observations

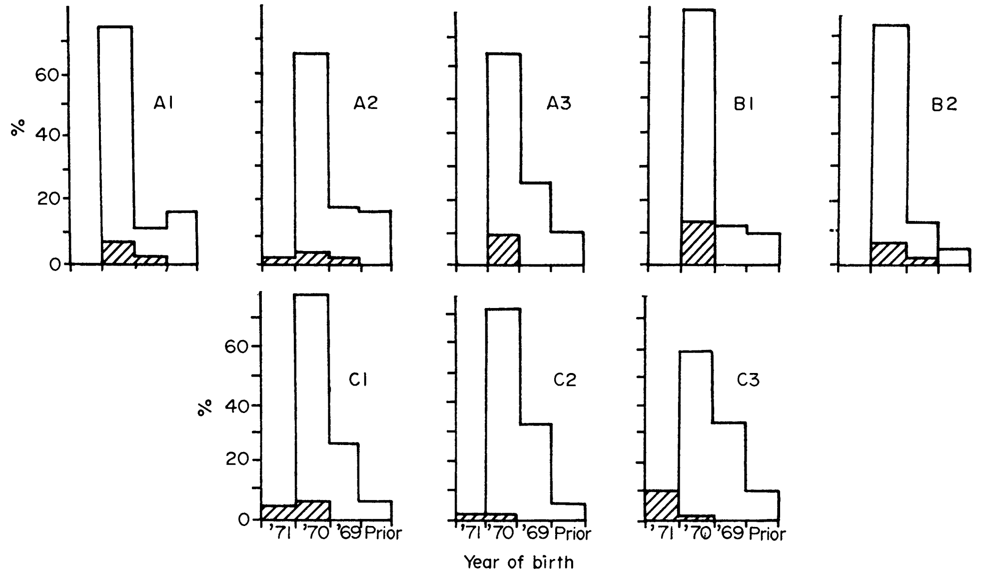

FIG. 9. Age distribution of the living plants of *Ranunculus repens* at April 1971 in eight 1 m^2 populations. Hatched areas indicate plants originated from seed, the rest are plants of vegetative origin.

(comprising two or three turnover cycles) would give a more accurate estimate of age distribution.

Survivorship of populations of mature plants

Table 7 and Fig. 11 contain information about the fates of all the plants present at the first recording of the permanent sites (April 1969). Most of the plants in these populations must have been produced during August and September 1968; a small proportion might have originated in 1967 and 1966. The youngest ramets, at the first recording, were *c.* 30 weeks old.

There are two chief points to be noticed in the graphs of survivorship in Fig. 11. First, an overall exponential decrease in numbers with time and, second, an annual rhythm of mortality around the overall exponential decay.

Table 11. *Distribution of the ages attained by plants of* Ranunculus repens *which were born and died during the study (figures under each category and the number of plants originating from seed or vegetatively are percentages of the total number of plants observed)*

	Age attained at death (years)					Origin		Total
Site	0–0·5	0·6–1·0	1·1–1·5	1·6–2·0	2·1–2·5	Vegetative	Seed	
A1	53·2	41·0	2·6	3·2	0	56·1	43·9	310
A2	37·7	43·2	11·7	6·6	0·8	71·2	28·2	257
A3	34·8	53·3	2·2	9·2	0·5	70·9	29·1	227
B1	37·6	52·8	5·0	4·6	0	70·6	29·4	218
B2	55·2	35·1	3·5	5·3	0·9	44·7	55·3	114
C1	42·9	41·8	5·7	8·1	1·5	79·1	20·9	459
C2	34·4	55·6	2·4	6·8	0·8	86·8	13·2	410
C3	38·4	44·2	8·1	9·3	0	67·4	32·6	86

All survivorship curves for mature plants of *R. repens* conform to the exponential model: the plants face a risk of mortality of the same annual magnitude throughout their lives. An inspection of the early stages of life of ramets, not covered by studying the April 1969 populations, shows (Fig. 12) that from the very beginning of their life, ramets are exposed to a constant annual death risk. This constant annual risk is, however, unevenly spread within the year and the seasonal cycle which is superimposed on the constant annual decay rate provides some evidence of the way in which plant numbers may be regulated.

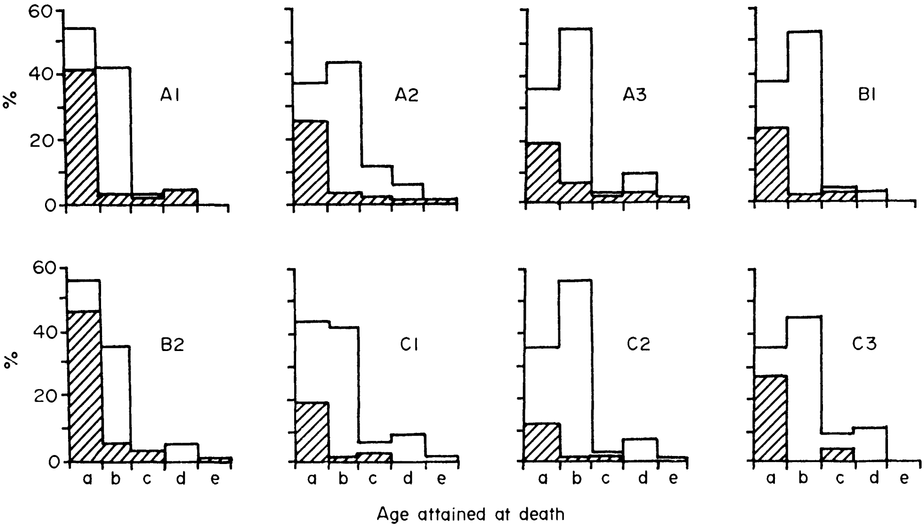

FIG. 10. Histograms of the distributions of ages attained at death by plants born during the study in populations of *Ranunculus repens*. Hatched areas represent plants originated from seed. Age-classes: (a) 0–0·5; (b) 0·6–1·0; (c) 1·1–1·5; (d) 1·6–2·0; (e) 2·1–2·5 years.

Lotka (1925) refers to the probability of a plant born at time N_o surviving until time N_a as

$$N_a = N_o\, p(a)$$

where $p(a)$ is the probability (N_a/N_o) of a plant surviving the period of time $(a\text{–}o)$. The derivative of this relationship becomes

$$\frac{dN_a}{da} = -\mu_a N_a$$

or

$$-\mu_a = \frac{dN_a}{N_a da} = \frac{d \log_e N_a}{da}$$

where μ_a is defined by Lotka as the 'force of mortality' at age a. This force of mortality measures the rate of decay or death in the population in an interval of time. By calculating the rate of decay of the population at each time interval as

$$\frac{\log_e x_n - \log_e x_{n+1}}{t_{n+1} - t_n}$$

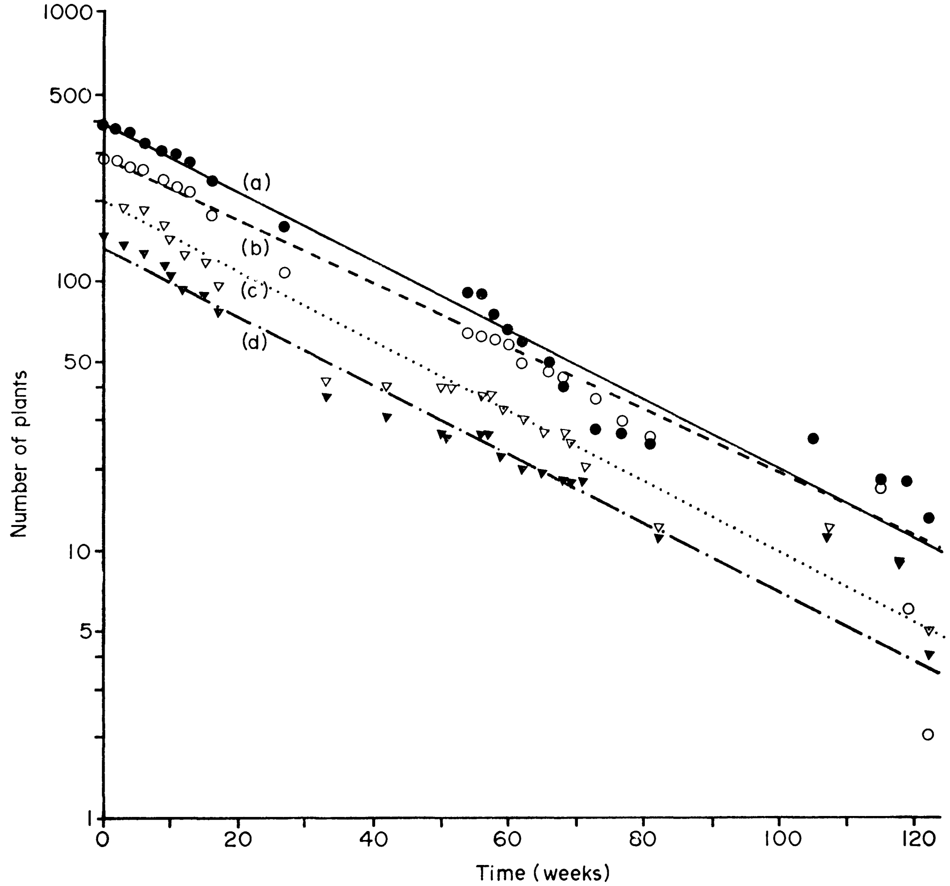

FIG. 11. Survivorship of four populations of *Ranunculus repens* in permanent sites of 1 m^2; time in weeks after first observation (April 1969). Sites: (a) A1, ●; (b) A2, ○; (c) C1, ▽; (d) C2, ▼.

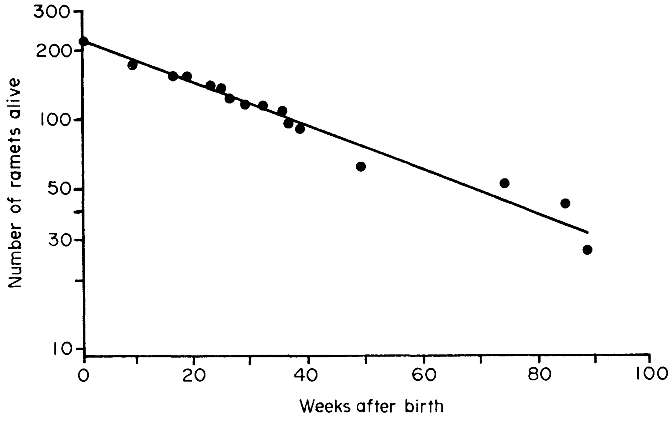

FIG. 12. Survivorship of a population of vegetative propagules of *Ranunculus repens* born at the same time (summer 1969), showing exponential decay from the early ages (site C1). Compare with Fig. 11(c).

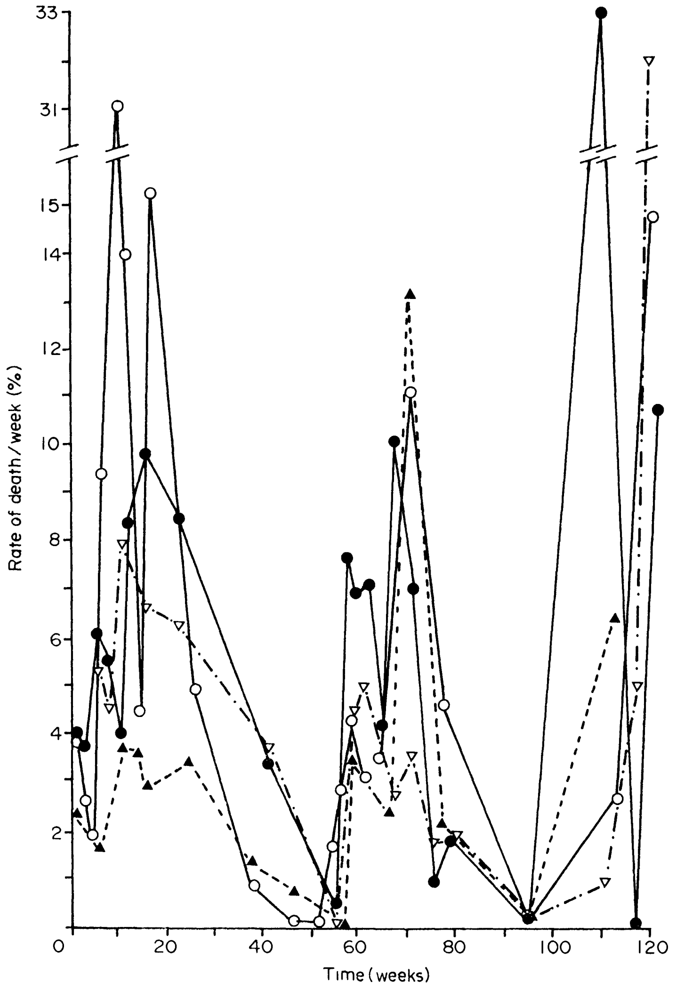

FIG. 13. Rate of death per week of mature plants of *Ranunculus repens*. Site A1, high density, intense grazing (●—— ●); site A3, low density, intense grazing (▽ ·—· ▽); site C3, low density, light grazing (▲ - - - ▲); site C2, high density, light grazing (○—— ○).

where x_n = surviving plants at time n and $t_{n+1} - t_n$ is the time interval considered, a measure of the severity or 'force' of mortality at different times during the year is obtained. The percentage rate of death of plants per week in four sites (A1, high density, intense grazing; A3, low density, intense grazing; C2, high density, light grazing; and C3, low density, light grazing) has been plotted against time in Fig. 13.

Large differences in the risk of death can be seen within the yearly cycles, as well as consistent differences between the types of site. A period of very heavy mortality between April and October was followed by a phase of low mortality from October onwards; a minimum value (zero mortality in many cases) was reached just before April in the following year. In both years all the sites studied showed a consistent very conspicuous trough in the middle of the spring–summer peak of mortality.

In those plots at high population density that were only lightly grazed, plants of

R. repens suffered severe mortality during the active growing season; plants in sites of lower density or intensely grazed were apparently at less risk.

Survivorship of populations of seedlings

Populations composed mostly of mature plants or exclusively of ramets suffered a repeating pattern of mortality risk, independent of age. The survivorship of seedlings seems to be markedly different. Because of the scarcity of seedlings of *R. repens* emerging at the same time in an area, it was necessary to examine for each site all the seedlings that were born and died during the study, computing the age at which each plant died. One example of the age distribution at death of a population recruited from seed is illustrated in Fig. 14 (cf. Fig. 12). The data suggest that the mortality was more severe in the early life stages. However, because of the small number of individuals involved and the short time of observation it is difficult to say whether the drop in number of surviving plants shortly after germination was due to a mortality risk peculiar to seedlings or simply reflected the same seasonal rhythm in mortality that was observed in the mature populations.

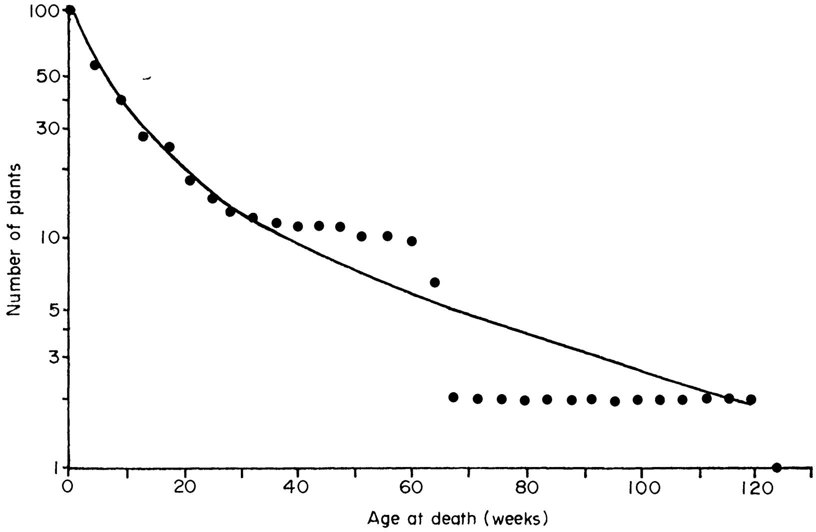

FIG. 14. Age at death of plants in a population of *Ranunculus repens* originated from seed at different dates during the study (numbers in old-age categories are under-represented).

The life expectancy of individuals of known age

Let us assume that in a population that has been studied for a given period, the expectancy of further life of plants that were born during the period and still survive does not differ markedly from that of individuals in the total population observed. Then, life expectancy would be

$$\frac{\text{total time lived by individuals in the period}}{\text{total individuals born in the period}}$$

or, expanding,

$$\frac{\begin{array}{c}\text{time lived by individuals completing their lives in the period observed}\\ +\ \text{time lived by the surviving individuals up to the end of the period}\\ +\ \text{their expectancy of further life } (L)\end{array}}{\text{total individuals born in the period}}$$

which gives an approximation to life expectancy, L, assuming that L for the living individuals is equal to L of the individuals that died.

Let n_x be the number of individuals living up to time x and dying during the study and n'_y the number of surviving individuals that attain an age y at the end of the study, then,

$$L \approx \frac{\Sigma n_x . x + \Sigma n'_y . y + L\, \Sigma n'_y}{\Sigma n_x + \Sigma n'_y}. \tag{1}$$

Solving eqn (1) for the desired unknown L,

$$L\left(1 - \frac{\Sigma n'_y}{\Sigma n_x + \Sigma n'_y}\right) \approx \frac{\Sigma n_x . x + \Sigma n'_y . y}{\Sigma n_x + \Sigma n'_y},$$

and

$$L \approx \frac{\Sigma n_x . x + \Sigma n'_y . y}{\Sigma n_x}.$$

Thus, the final form of the estimation of life expectancy becomes the time-individual lived by the fraction of the population that dies plus the time-individual lived up to the end of the period of observation by the surviving population, divided by the total number of individuals observed to die in the study.

By use of the previous formula, life expectancies were calculated for all individuals of known age in each site and are presented in Table 12. The L values fluctuate only between 1 and 1·2 years except in the extreme sites of high *R. repens* density combined with intense grazing (A1 with $L = 0{\cdot}9$) and of low density combined with light grazing (C3 with $L = 1{\cdot}5$ years).

Because the survivorship curve of the populations recruited from seed appeared to be quite different from that of the populations of mature plants separate calculations for all seedlings and vegetative propagules of known age were made. These are included together with the life expectancies for the whole population in Table 12. The life expectancy of plants originating from seed varied between 0·2 years (just over 10 weeks) to 0·6 years (32 weeks) compared to that of the vegetatively produced plants which oscillated more widely from 1·2 to 2·1 years. The expectation of life of the vegetative propagules appeared to be density-dependent: Fig. 15 shows a significant trend ($P = 0{\cdot}05$) towards reduction of L with increasing densities.

These data illustrate clearly that seed production is a low-cost investment but with high risk and occasionally very high returns. The transition of an individual from the relatively safe dormant seed to a phase of intense physiological activity in which it is vital to have a positive balance in the photosynthesis–respiration budget is a very risky process.

Ramets, on the other hand, are produced at a much higher price, in a system that seems to regulate their longevity by the density of its own numbers. Vegetative daughters are supplied with the organs, the nourishment and often the space, necessary to become safely established.

An average vegetative daughter can expect to survive for at least one full growing season after having been produced. Vegetative daughters in a low density population (e.g. site C3) lived one growing season longer than those present in a high density population (e.g. site C1).

Table 12. *Comparison of the life expectancies* (L) *for all individuals of known age and for plants originating from seed or from vegetative reproduction in* Ranunculus repens (L *values in years*)

	Sites							
	A1	A2	A3	B1	B2	C1	C2	C3
All plants	0·9	1·2	1·1	1·2	1·0	1·0	1·1	1·5
Seedlings	0·2	0·3	0·6	0·6	0·4	0·4	0·3	0·3
Vegetative propagules	1·4	1·6	1·4	1·5	1·8	1·2	1·3	2·1

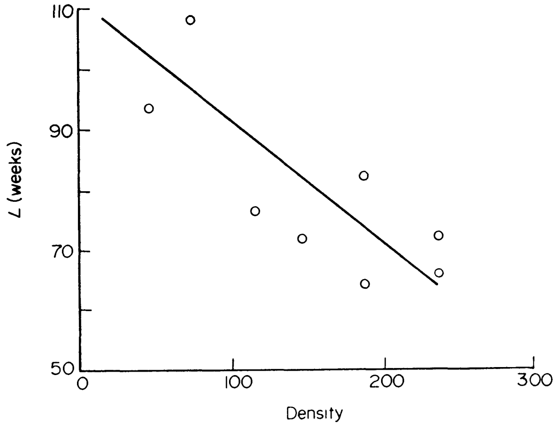

FIG. 15. The relationship between the life expectancy (*L*) of vegetative propagules of *Ranunculus repens* and the density of this species. Densities are averages of the number of plants/m^2 observed at each site in April 1969, 1970 and 1971.

R. bulbosus

Population flux

The densities of *R. bulbosus* in the experimental field were lower than those of *R. repens*, (see Table 5) ranging from 21 to 101 in April 1969 and from 32 to 193 in April 1971. The average density for the ten sites containing *R. bulbosus* increased from 55 to 82 plants/m^2 over the 2-year period. 'Poaching' during the 1969–70 winter affected especially sites E and F where the mature populations were reduced by up to 80% and virtually none of the plants which had germinated some 10 weeks previously survived to the next spring. The average population density of the ten sites in April 1970 fell to 33 plants/m^2 and in one site (F2) only two plants survived.

Several sites (e.g. F2) showed an extraordinary flush of germination in the autumn of 1970, considerably increasing the population size at some sites (up to 560% in the case of site F2). This did not appear to be related to the trampling in the preceding winter since not all trampled sites had high seedling populations and some of the sites which escaped trampling also bore large numbers of seedlings.

Changes in net population size are shown in Fig. 16. Losses in most cases were preceded by a period of seedling recruitment during the autumn; this was most clear in 1970. The magnitude of new recruitment did not appear to be related in any way to the earlier density of buttercups at the sites. The percentage survival of the populations present in

April 1969 at different sites showed wide variations (see Table 5). As a consequence, the estimated time necessary to complete a turnover varied from 2 to nearly 5 years with an exceptional figure of 10 years (site G2). The non-trampled sites showed a higher percentage survival than those trampled, so probably the 'normal' turnover time was nearer to 4 or 5 years (sites B3, G1 and G3). Average annual mortality did not vary greatly, averaging 60% with extremes of 47 and 75%.

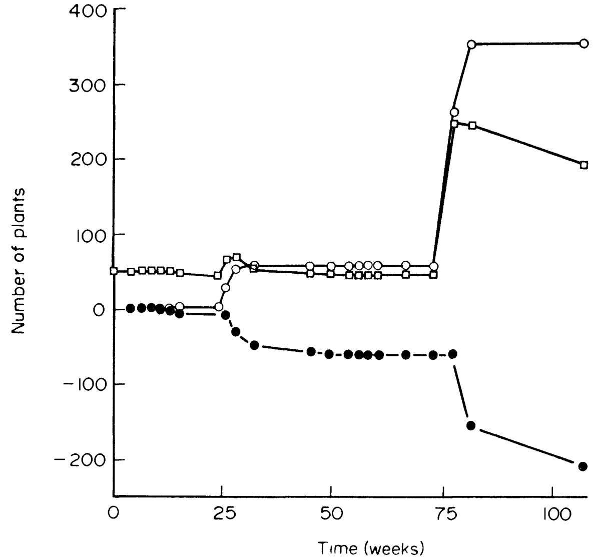

FIG. 16. Changes in population size of *Ranunculus bulbosus* (plants/m^2) at site G2. ○, Cumulative gains; ●, cumulative losses; □, net population size.

Age structure of the living population

Because of the low rate of turnover and the effects of trampling on the seedling population of 1969, very little can be concluded from the available data about the age structure of the living populations of *R. bulbosus* in April 1971. Table 13 shows the proportion of the population represented by (a) plants living in the sites when the study was started, (b) plants older than 1 year (i.e. originated in the autumn of 1969), and (c) plants younger than 1 year (i.e. those emerged in the autumn of 1970).

The high proportion of young plants in many of the sites was due to the remarkable flush of germination in 1970 following heavy mortality in the winter of 1969. An extreme example is seen in site F2, where only one plant from the original 1969 population survived to April 1971, and 302 seedlings germinated during the second year.

Age distribution of dead plants

As a consequence of the factors that affected the age structure of the living population, the age distribution of the plants which died during the study was very irregular. Table 14 shows that all the mortality observed during the study was of plants less than 1 year old (most of them died at age 1–3 months).

About 60% of the plants whose birth was recorded during the study also died within that period, all of these being less than 1 year and most of them less than 3 months old.

No mortality was recorded of plants between 1 and 2 years old because the seedling crop of 1969 has been drastically reduced. Most of the rest of the plants of known age were recruited from the 1970 season of germination.

Table 13. *Percentage representation by plants of different ages in populations of* Ranunculus bulbosus *in April* 1971

	Sites									
Born	B3	E1	E2	E3	F1	F2	F3	G1	G2	G3
Prior to 1969	58·3	41·7	48·7	15·9	11·2	0·7	56·2	64·1	20·7	23·3
1969	12·5	11·1	7·7	6·8	0	0	0	7·8	1·1	2·5
1970	29·2	47·2	43·6	77·3	88·8	99·3	43·8	28·1	78·2	74·2

Table 14. *Proportions of plants of* Ranunculus bulbosus *as a percentage of the total number of plants of known age that died* (*a*) *younger than* 1 *year*, (*b*) *between* 1 *and* 2 *years old, and* (*c*) *that were still alive at the end of the study*

	Sites									
	B3	E1	E2	E3	F1	F2	F3	G1	G2	G3
(a) Dying younger than 1 year old	81·5	43·2	43·2	47·2	54·1	61·9	67·5	71·8	56·8	50·8
(b) Dying between 1 and 2 years old	0	0	0	0	0	0	0	0	0	0
(c) Alive at the end of the study	18·5	56·8	56·8	52·8	45·9	38·1	32·5	28·2	43·2	49·2

Survivorship of populations of mature plants

Survivorship curves for the populations of mature plants of *R. bulbosus* present in April 1969 are presented in Fig. 17; the basic data are given in Table 8. There are again indications of a seasonal rhythm of mortality imposed on a generally exponential decay, but the situation is less clear than for *R.repens.*

The seasonal variations in the rate of death are shown in Fig. 18, for sites of varying density and intensity of grazing. Mortality reached a peak in April and again in May, separated by a narrow trough which coincided with the flowering season; after May the mortality risk slowly declined and in some cases was zero between July and August. This period corresponded with the shedding of the above-ground structures of the plants and the beginning of the summer rest. Although this is a fairly safe period for the plants some mortality probably occurred when the corms were dormant, since a number of plants, mainly in sites subjected to intense grazing, were not observed to re-sprout in the following autumn. From September onwards, with the initiation of new leaf growth, mortality increased steadily until it reached a peak in April. In marked contrast with *R. repens*, there was appreciable autumn and winter mortality: it may be that the remobilizing of reserves and the development of new leaves in autumn and of a new corm in late winter (processes which require physiological activity) represented a considerable stress for the plants and consequently reduced their chances of survival.

Survivorship of populations of seedlings

The survivorship curve of seedlings is clearly different from that of established plants. The seedling populations that originated in the autumn of 1969 were analysed and the

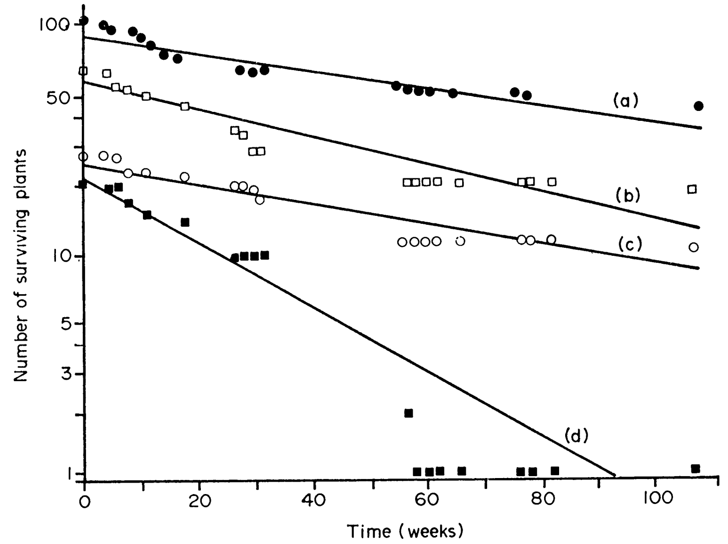

FIG. 17. Survivorship of populations of *Ranunculus bulbosus* in 1 m^2 permanent sites; time in weeks after first observation (April 1969). Sites: (a) B3, ●; (b) F3, □; (c) F1, ○; (d) F2, ■.

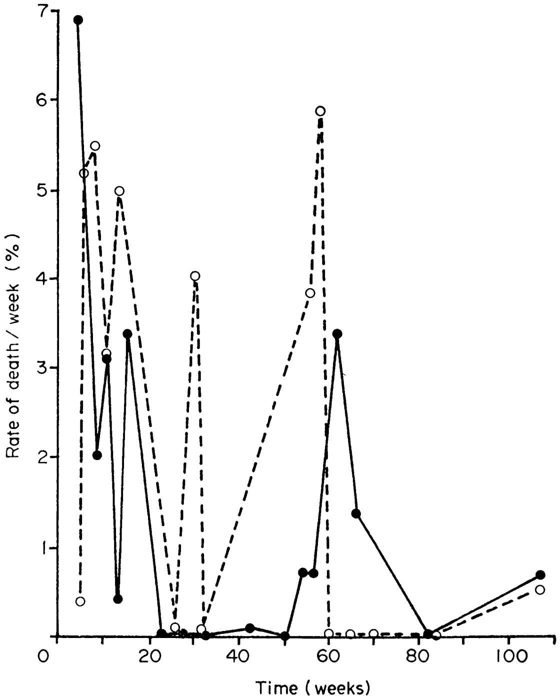

FIG. 18. Rate of death per week of mature plants of *Ranunculus bulbosus*. Site G1, high density, light grazing (●); E3, low density, intense grazing (○).

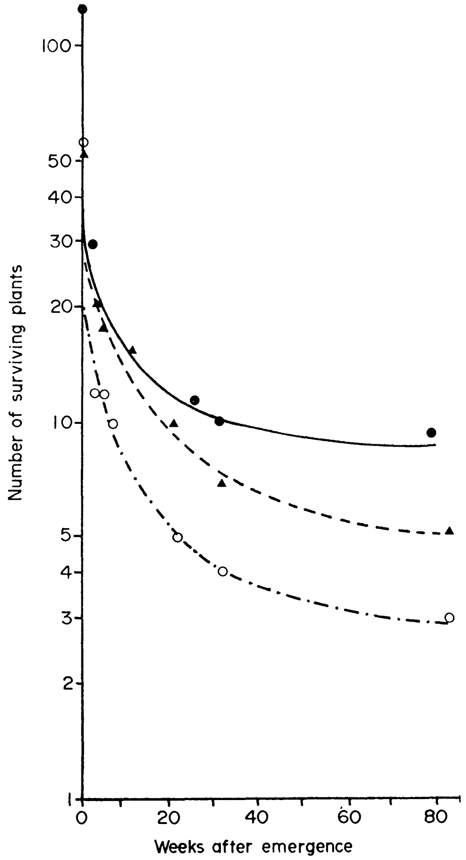

FIG. 19. Survivorship of three populations of seedlings of *Ranunculus bulbosus* that emerged simultaneously in the autumn of 1969 (recorded in three permanent plots of 1 m^2). ●, Site B3; ▲, site G2; ○, site G1.

trampled sites were disregarded since they showed an abnormally high mortality during the 1969–70 winter. Fig. 19 shows data for three 1 m^2 sites in which a very rapid decrease in the numbers of seedlings during the first 20 weeks after emergence (up to late March) was noticeable. After this date, the mortality risk was very similar to that of the mature populations.

R. acris

Population flux

This species was the most widespread of the three buttercups in the field studied but very seldom formed dense populations. Nearly all the twenty-one plots of 1 m^2 included at least some plants of *R. acris*.

Five of the *R. acris* sites were chosen for detailed analyses; two (D2 and D3) had high densities of *R. acris* but the other two species were rare or absent, one site (A2) bore a low density of *R. acris* together with *R. repens* and in two of the sites (B3, G2) *R. bulbosus* predominated (see Table 6).

Because the first observation on populations of *R. acris* coincided with the onset of germination in this species, the populations present in April 1969 were composed of

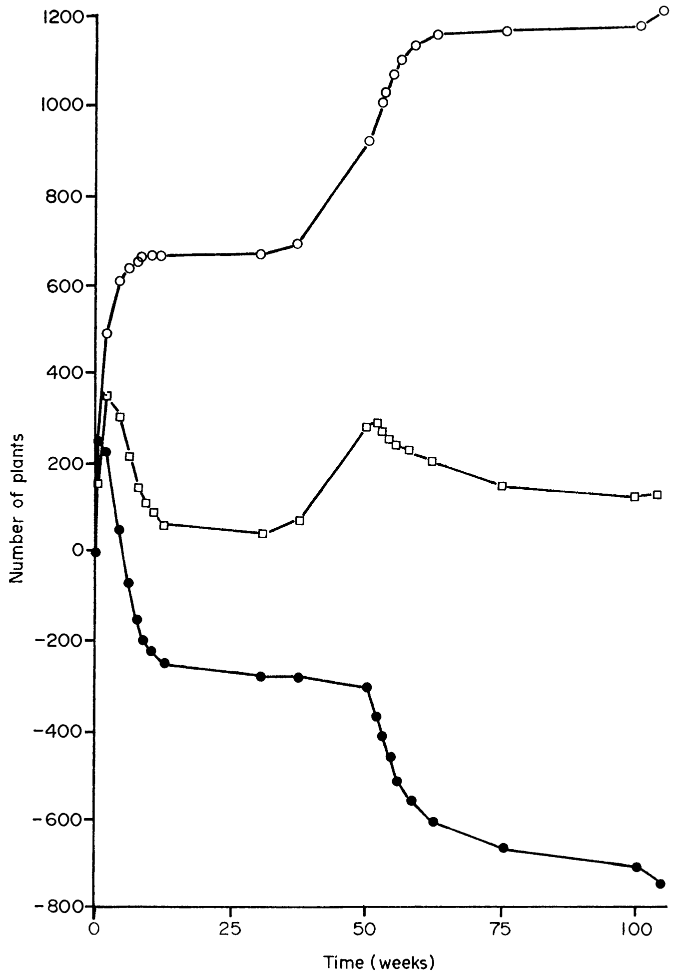

FIG. 20. Changes in population size of *Ranunculus acris* (plants/m^2) at site D2. ○, Cumulative gains; ●, cumulative losses; □, net population size.

mature plants plus a large number of seedlings and young plants. Only the mature populations have been considered as the 'original' for April 1969, the seedlings being treated as new recruits for the analysis of population trends.

In sites in which *R. acris* was the only buttercup species present its population behaved very differently from those where the species grew mixed with other buttercups. The original differences in density between the plots (13–143) had become even greater at the end of the study (1–333). The populations at the 'pure' *R. acris* sites (D2, D3) increased to 2·0–2·3 times their original size, while in the mixed species sites (with low densities), the populations became even smaller, and in site B3 there were four complete turnovers of population of different size during the 2 years of study. A series of small and ephemeral populations established and overlapped in time with each other so that the species was always represented in the sites but by strictly temporary occupants. This situation was common in most of the sites in which the other two buttercup species were abundant and where the populations of *R. acris* were small.

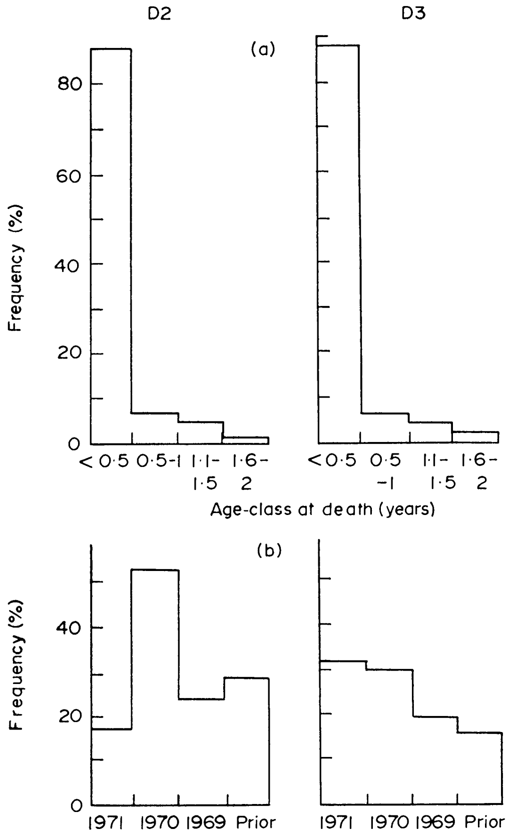

FIG. 21. Age distribution of populations of *Ranunculus acris:* (a) for plants alive at the end of the study; (b) for plants born and died during the study.

Percentage survivorship of the original populations in the pure *R. acris* sites and that dominated by *R. repens* (A2) were very similar and the expected time for turnover in these sites varied little (4·3–4·0 years); in the other two sites (B3, G2) there was a lower survivorship rate and a shorter expected time for turnover: 2·4 years for site G2 and 0·4 years in site B3 where four turnovers were observed. The same pattern is seen in the percentage mortality of all plants, which was *c.* 76% in sites D2, D3 and A2 but much higher in the other two sites.

R. acris is outstanding among the three species of buttercups as an example of the vast numbers of plants that may be involved in the population flux in a single square metre in only 2 years (Fig. 20). In site D2, 1350 plants were recorded between April 1969 and April 1971; 518 plants were recorded for the same period in site D3.

The gains, especially in 'pure' *R. acris* sites, were spread over several months, from February or March up to the end of June though germination reached a peak between mid-March and mid-April.

In both 'pure' *R. acris* sites the population size was always kept above the original density recorded, so there was not a single loss-dominated period.

Age structure of the living population

The only sites suitable for an examination of the age distribution of the population present at the end of the study were D2 and D3. D3 had a relatively stable distribution but D2 showed marked discontinuities (see Fig. 21a). The relatively low number in the first age category reflects the considerably lower germination in 1971 compared with 1969 and 1970. The uneven age-distribution in D2 would probably affect recruitment when the class of 1971 became a part of the reproducing fraction of the population.

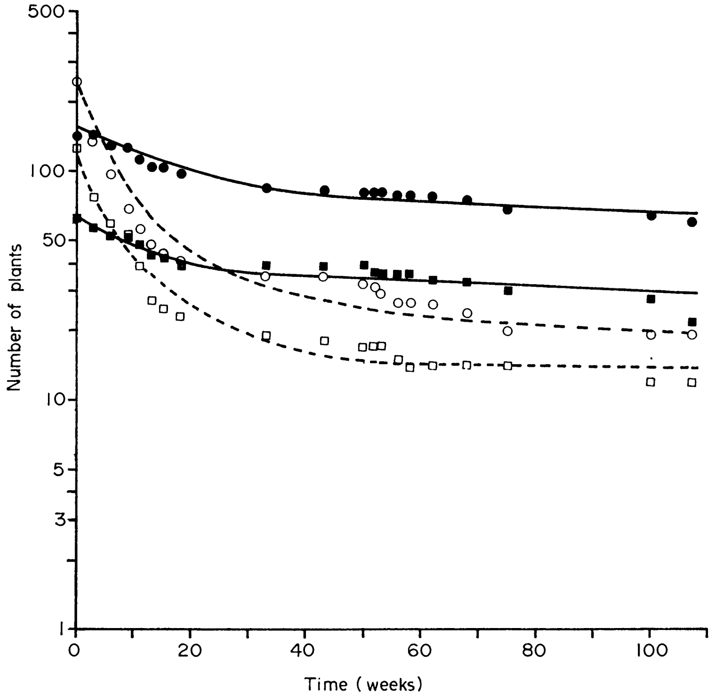

FIG. 22. Survivorship of populations of *Ranunculus acris* in 1 m^2 permanent sites; time in weeks after the first observation (April 1969). Survivorship of mature plants: site D2 (●—— ●) and D3 (■—— ■); survivorship of seedlings emerged in April 1969 in site D2 (○ – – – ○) and site D3 (□ – – – □).

Age distribution of dead plants

The age attained at death by plants of known age in sites D2 and D3 (Fig. 21b) illustrates clearly the greater risk of deaths in the early stages of life. More than half of the plants dying in age-class 0–0·5 years died during the first 3 weeks after germination. Just before the completion of the first half-year of life the mortality risks were greatly reduced and remained at a low level thereafter. If allowance is made for the under-representation of plants in older categories, it appears that the mortality risk after the first six months from germination became fairly constant.

Survivorship of populations of mature plants

Mature populations of *R. acris* show an overall exponential decay. The initial steeper part of the curve, drawn in Fig. 22 for sites D2 and D3 respectively, was very probably due to the inclusion of a number of recently germinated seedlings as mature plants. These young plants, as discussed later, suffered a greater mortality risk and produced a survivorship curve similar to Deevey's type III; after the first 10 weeks of observation, survivorship of the mature populations attained a clearer exponential trend.

The rate of death of the populations within each year showed a clear seasonal trend (Fig. 23), as with *R. repens* and *R. bulbosus*. The mortality peak in *R. acris* populations was restricted to the period May–July, after which mortality was maintained at very low levels until the next spring. Within the spring peak of mortality, a trough occurred at the beginning of June in 1969 but it was not so clearly defined in the following year. The relatively higher mortality in 1969, followed by 2 years of similar lower mortality, reflected the inclusion of a number of non-mature plants as part of the mature population in 1969.

Populations of *R. acris* in sites with a predominance of *R. repens* or *R. bulbosus* behaved differently from those sites where *R. acris* was the predominant buttercup; this suggests that there may be interactions between the three species and that the intraspecific regulation of mortality may differ greatly from regulation in the presence of large numbers of another species.

The other site considered (G2) in which *R. bulbosus* was the predominant species illustrates the argument for a possible differential regulation of mortality within and between species. *R. acris* in this site had greater mortality at times when the 'pure' *R. acris* sites showed the lowest mortality and *vice versa*. Mortality in this low density site, instead of being concentrated in the period April to July, extended well beyond September. The mid-spring trough in mortality was also noticeable, in 1969 as complete survivorship from mid-May to mid-July and in 1970 as a reduction of mortality in early May and in early June. The mortality peaks for this site in both years are very similar.

Survivorship of populations of seedlings

The large numbers of seedlings produced in the 2 years in sites D2 and D3 provide a good picture of the survivorship of plants at early stages. The fates of the 1969 seedling crops in these sites are illustrated in Fig. 22, together with the corresponding survivorship data from the mature populations. Seedlings suffered a high mortality risk immediately after germination; this became gradually less severe with increasing age. Between the twentieth and thirtieth week of age (September to October), the mortality of plants derived from seed followed the same trend as that of the mature populations. The 1970 seedling crops behaved similarly.

The life expectancy of individuals of known age

In the case of *R. acris* the large number of plants of known age that were recorded permitted a calculation of their approximate life expectancy L. By use of the data from all the individuals that appeared during the study, a value of $L = 24{\cdot}4$ weeks was obtained for individuals in site D2 and $L = 26{\cdot}7$ weeks in site D3. However, in populations where there was a large difference in mortality at different ages, L at birth gives very little information about the chances of further life of those individuals which survived to greater age. A calculation of L at different stages in the life of the individuals becomes necessary in order to gain an understanding of the mortality process in older individuals. Life expectancy for individuals of *R. acris* in both plots (Fig. 24) increased from 0·5 years at birth to 2·2 years for plants living up to 6 months and increased again to 3·8 years for those plants which achieved 1 year of age. The values obtained for plants 1·5 years old or older appear unrealistically high and further observations are needed for a better estimation of the life expectancies of plants more than 1 year old.

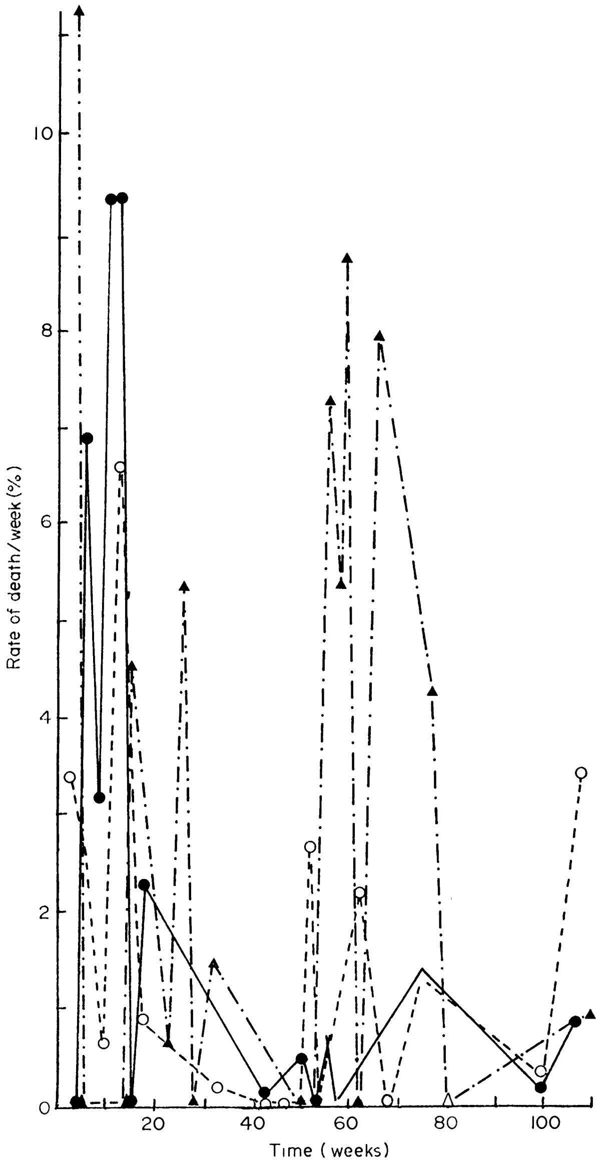

FIG. 23. Rate of death per week of mature plants of *Ranunculus acris*. Site D2 (●—— ●) and D3 (○ - - - ○), high density and light grazing; site G2, low density, light grazing (▲ -·- ▲).

GENERAL DISCUSSION

Populations of mature plants of *Ranunculus* spp. appeared to exhibit a negative exponential type of mortality, i.e. Deevey's type II, a conclusion in line with the very scanty information available for other species (Tamm 1948, 1956; Rabotnov 1956, 1958; Sagar 1959; Antonovics 1966, 1972).

A general comparison of the longevity of the three species of *Ranunculus* shows that life

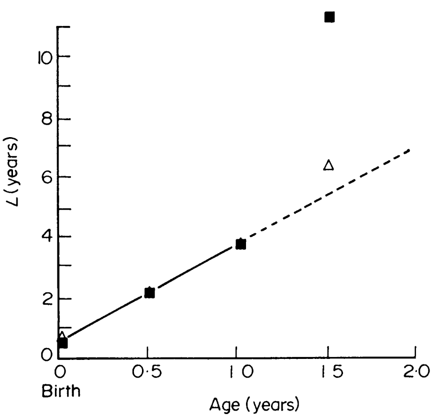

FIG. 24. Increase in further expectancy of life (*L*) with the increase in age of plants of *Ranunculus acris* born from seed. Data from the total population of known age in two 1 m^2 permanent plots. Site D2 (■); site D3 (△).

expectation, at the time of birth, within the population considered as a whole, is considerably higher in *R. repens* than in *R. acris* or, very probably, *R. bulbosus*. However, if mature established plants are considered, the expectation of life of the last two species is much greater than for *R. repens*. A high toll of genet mortality is paid by *R. acris* and *R. bulbosus* at the beginning of their physiologically active life, but it is rewarded with a long life for those individuals that succeed. *R. repens* suffers little loss of ramets at the beginning of their life but it replaces a large number more often.

To illustrate graphically how mortality operates at different times during the life of the buttercups and therefore what the expectations for further life are at different ages, the age-specific death rates of all plants of known age of one population of *R. repens* and *R. acris* have been calculated and shown in Fig. 25.

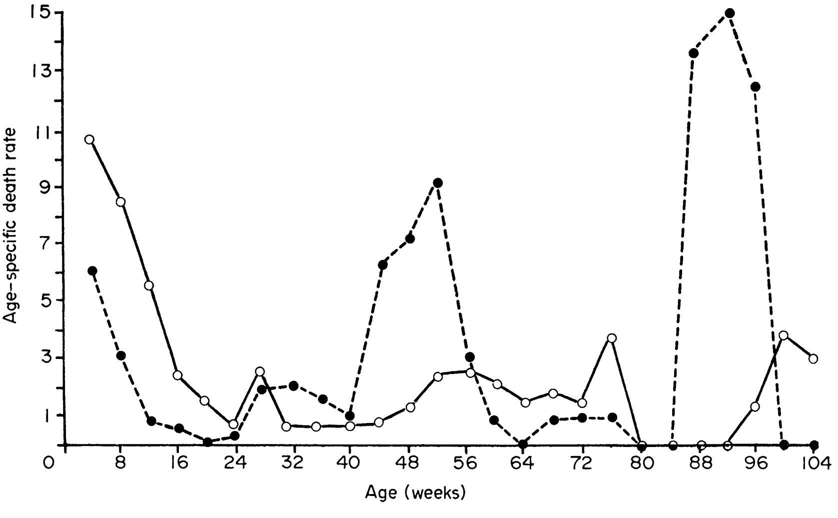

FIG. 25. Age-specific death rates for one population each of *Ranunculus repens* and *R. acris* observed in two different 1 m^2 permanent plots during 2 years.

Age-specific death rates are calculated as:

$$\frac{\text{no. of plants dying in age class } x}{\text{total no. of plants observed which attain age class } x}.$$

The age-specific death rate of age-class 0–4 weeks, for example, is

$$\frac{\text{no. of plants dying between 0 and 4 weeks old}}{\text{total no. of plants observed to attain 0 to 4 weeks of age (i.e. all plants of known age)}}.$$

Both species suffered a relatively high death rate at the first 8–12 weeks of age. Mortality at this stage was twice as high in *R. acris* as in *R. repens*. After the 16th week, *R. acris* attained a remarkably constant age-specific death rate up to the 76th week (1·5 years). From this time onwards, oscillations in age-specific death rate became wider. *R. bulbosus* appears to behave in a similar fashion.

High death rates in the first weeks of life of *R. repens* were largely due to seedling mortality. If the vegetative propagules alone are considered, the death rate at these ages was only *c.* 1–2% per week. Two noteworthy peaks of mortality at 52 and 92 weeks (approximately 1- and 2-year-old categories) show the effects of increased mortality during the active growth period in spring and early summer. However, mortality between these peaks remained low and rather constant.

Calculated death rates after 1·5 years (76 weeks) are probably exaggerated for both species since it is possible that the number of plants that would live to greater age (> 1·5 years) was under-represented because the observations extended only for 2 years.

The analysis of mortality in mature populations of the three species shows clearly that the highest death rates occur during spring and early summer (i.e. when active growth of the sward is taking place) and not during the winter months, or the drier late-summer period. This suggests that mutual demands for limited resources may be to a large extent responsible for regulating the mortality of the three species and that the rigours of climate play only a minor role in this regulation. Perhaps surprisingly, in all the studies quoted above, there is a relentless, rather constant annual risk of death which suggests that climatic variations are not important in controlling plant numbers.

Very few studies on other plant species elsewhere relate mortality to any parameter of the growth rate of survivors. Those made by Lamp (1952) on *Bromus inermis*, Langer (1956) on *Phleum pratense*, Langer, Ryle & Jewiss (1964) on *P. pratense* and *Festuca pratensis* and Robson (1968) on *F. arundinacea* provide interesting evidence that the intense process of growth of plants in a population may be a major factor affecting survivorship. In all these studies, where the species were grown in pure stands, it was found that the mortality of tillers increased sharply and attained a maximum at the time of maximum growth of the species. Langer (1956) showed that flowering tillers of *Phleum pratense* have smaller chances of survival than vegetative tillers. His data also show (Fig. 26b) that the higher mortality risk for tillers occurs shortly after maximum dry matter production has been attained. The season at which this maximum mortality occurred varied with the time at which the tillers had been produced. Those produced before June of one year have a maximum mortality in August of the same year. Those born from June onwards apparently escape the effects of active growth in that year and show a maximum of mortality in August of the following year.

Mortality, birth rates and longevity are critical elements of the life cycles of species. A balance, resulting from complex interactions between the three, must be obtained if populations of a species are to maintain stability. It is not clear, from the data obtained in this study, whether mortality occurred as a result of the recruitment of new individuals or if recruitment resulted from the death of individuals.

The major periods of mortality in the mature populations of the three species of *Ranunculus* occurred during spring and early summer but were not synchronous. The process of mortality started earliest in populations of *R. bulbosus* which is the species that starts spring growth earliest (Fig. 27). The mortality of *R. acris* increased in mid-April and was closely followed by *R. repens* in early May. *R. bulbosus* suffered two periods of severe mortality, in mid-April and mid-July.

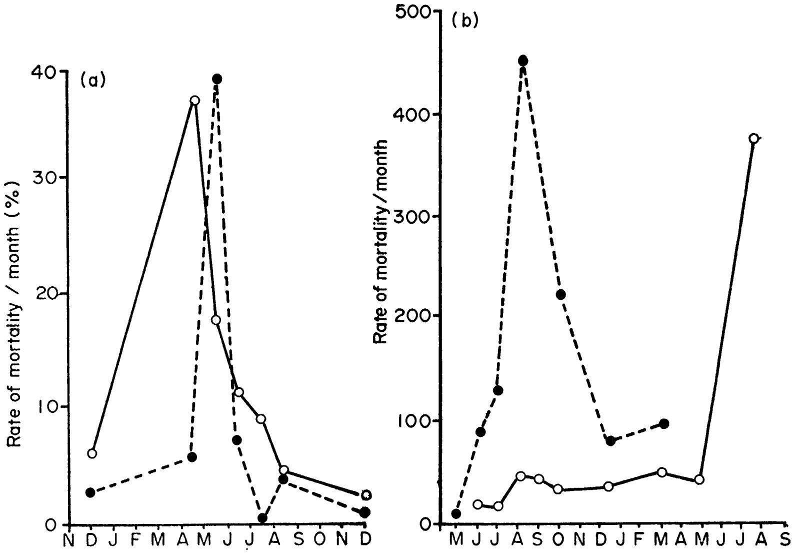

FIG. 26. (a) Percentage rate of mortality per month in populations of *Plantago lanceolata* observed in two 1 m^2 permanent plots in Oxfordshire. ○, Plot C; ●, plot D; calculated from data of Sagar (1959). (b) Rates of death of tillers of *Phleum pratense* produced in pure stands at different seasons during the year. Line common to all tillers produced before June 1951 (●), line common to all tillers produced between June 1951 and May 1952 (○). Adapted from Langer (1956).

A pre-reproductive peak of mortality occurred in all the species. It was earlier in *R. bulbosus* (mid-April) than in *R. acris* (mid-May) and *R. repens* (late May). A second, post-reproductive peak was also common to the three species and was greater than the pre-reproductive peak in *R. repens* and *R. acris*. Again it occurred earlier in *R. bulbosus* (mid-July) than *R. acris* (late July) and *R. repens* (mid-August).

The reduced mortality at the middle of the growing season corresponded in all three species with the time when the maximum number of plants were observed to flower. It occurred at different times for the three species: it was earliest in *R. bulbosus* (late May) which is the first species to flower; it occurred later in *R. acris* and *R. repens* (mid- and late June, respectively).

Some populations of *R. bulbosus* were an exception to this general rule having quite different mortality risks in the two years of the present study, although within each year mortality of mature plants was approximately exponential. However, these sites suffered a particularly severe disturbance from 'poaching' and it may be dangerous to generalize from them.

In *R. repens* and *R. acris*, but especially in the former, longevity (and turnover in consequence) seemed to be density-regulated.

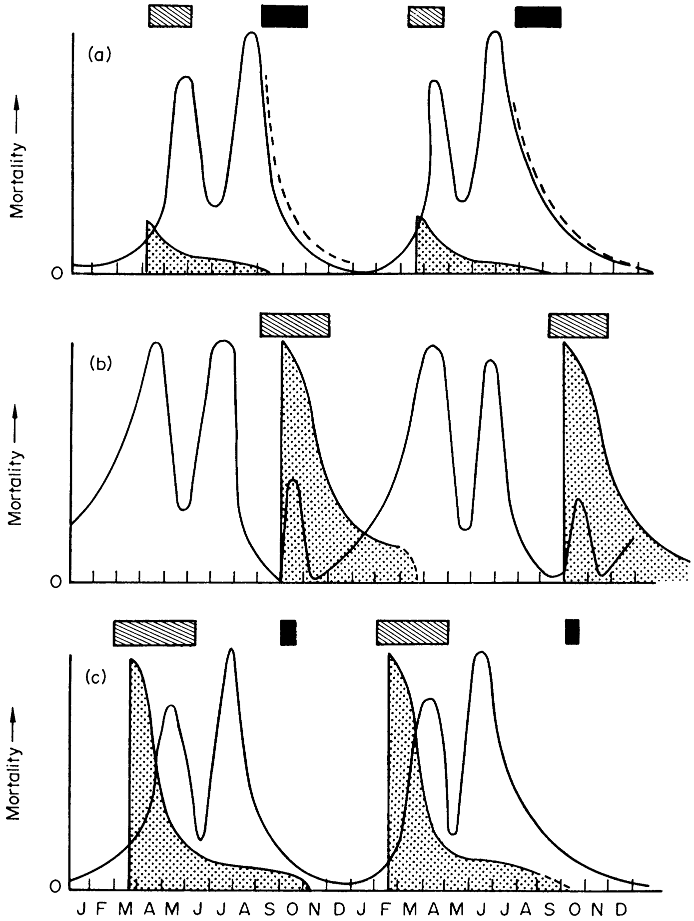

FIG. 27. Diagrammatic representation of the rates of mortality in populations of *Ranunculus repens* (a), *R. bulbosus* (b) and *R. acris* (c) at different times through the year. The continuous line represents mortality of mature plants; the shaded areas seedling mortality and the broken line the mortality of newly born vegetative propagules. Blocks show time of seedling recruitment (filled) and vegetative recruitment (cross hatched).

A full comparison of the longevity of genets of the three species cannot be attempted until more complete information about the life span of clones of *R. repens* is obtained. Plants of the three species undergo extensive morphological renewal each year. On average, rosettes of *R. acris* lived longer than those of *R. repens* or *R. bulbosus*.

Rabotnov's (1958) study of *R. acris* in the U.S.S.R. provides an extremely valuable opportunity for comparing the mortality risk of a species in widely different localities and environmental conditions. Survivorship data can be calculated from his published records for populations of *R. acris* in river meadows; these show almost exactly the same slope of exponential decay of mature plants to that obtained for the same species in the present study (Fig. 28). This suggests that the process of mortality, at least in its overall *modus operandi*, may not vary greatly for totally different populations of a given species.

An exponential loss of numbers from a population implies a constant risk of death. There was, however, a marked seasonal rhythm superimposed on the annual exponential death rate for the three species. Seasonal rhythms also occur in the death rate of populations of other grassland species. Natural populations of *Plantago lanceolata* show a similar rhythm of mortality (Fig. 26a). Antonovics (1972) found that the highest death rate in populations of *Anthoxanthum odoratum* occurred during the summer months, but could find no correlation with climatic conditions that could help to interpret the seasonal trends.

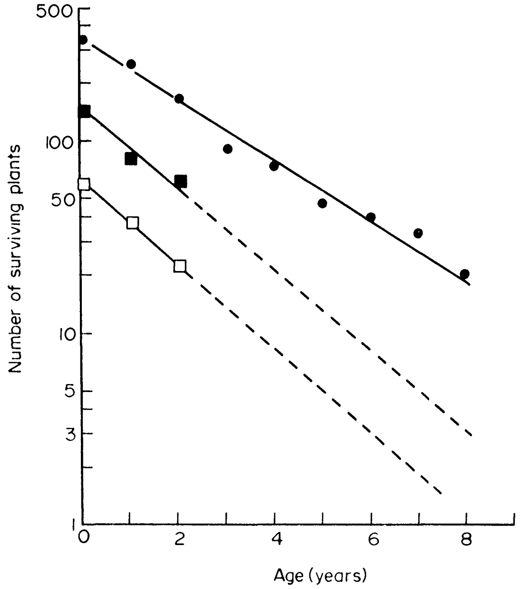

FIG. 28. Survivorship of populations of *Ranunculus acris*, obtained independently at two different localities. Oka River populations (●), calculated from data of Rabotnov (1958); Aber Farm populations, site D2 (■) and D3 (□).

The seasonal pattern of mortality of the newly recruited populations showed even greater differences between the three species. The mortality of the newly produced vegetative propagules of *Ranunculus repens* followed, from the beginning, the same rate of mortality as the mature populations (cf. Fig. 12). In contrast, the populations of newly emerged seedlings of *R. bulbosus* and *R. acris* showed high rates of mortality immediately after germination (cf. Figs. 19 and 22), and therefore constituted a distinct period of mortality in the population when considered as a whole. Seedling mortality occurs at very different times of the year: early in spring in *R. acris*, 2–3 weeks later in *R. repens*, and in autumn in *R. bulbosus*. Seedling mortality in *R. repens* was an insignificant part of the mortality of the whole population, but it is interesting that it occurred at a markedly different time of the year from that of the vegetative propagules (late summer).

Seedlings are clearly a highly vulnerable stage in the life cycle of the buttercups but represent the only way in which new genets are recruited to the population. The high risk of death at this stage may reflect not only the innate risks in establishing a viable root and shoot system but also part of the genetic load carried by the species. New genotypes are by their nature experimental and elimination of most of the unfit genotypes might be expected to occur early in their life.

Tested genotypes, represented by adult plants, may multiply clonally and have a relatively short ramet life (*R. repens*) or have relatively long-lived genets and little or no vegetative reproduction (*R. acris*, *R. bulbosus*). The evidence from the census of deaths is that the adult population does not suffer from the physical hazards of what are usually regarded as the harsh seasons but that the greatest risk comes during the active growing season. It is an interesting paradox in evolutionary theory that natural selection cannot optimize the number of descendants that an organism leaves—the fittest individual is the one that leaves more descendants than its fellows. Over-population is therefore bound to be a recurrent risk to animals and plants, and the evidence of density-dependence in the life expectancy of ramets in *R. repens* suggests that self-crowding is a cause of death. Niche diversification is successful if it permits a group of species to avoid the density stress that each creates and the marked asynchrony in the risk of mortality of the three species strongly suggests that their populations may be independently controlled.

The study emphasizes the great importance of mapping and frequent records in any study of the dynamics of a plant population. The relative stability of plant numbers within the plots conceals a very dynamic population flux which would have been completely obscured in a census of total population size made at yearly intervals: the dynamics of such a population can be assessed only by recording the individual behaviour of its members.

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SUMMARY

All plants, including seedlings, of *Ranunculus bulbosus*, *R. acris* and *R. repens* were subjected to census at intervals of a few weeks over 2½ years in an area of grazed pasture. Pantograph mapping enabled each individual in marked 1 m^2 quadrats to be identified at each census. Calculations were made of population flux, age distribution, age at death, the survivorship curve and life expectancy. Fluctuations in populations were small in comparison with the large number of individuals lost and gained (the flux). *R. repens* was the only species with appreciable vegetative multiplication. Seventy percent of the individual ramets of *R. repens* at the start of the growing season were 1 year old, 20% 2 years old, and the remainder older. Very few plants of *R. repens* from seedlings lived for more than 1·5 years. Seedlings accounted for 65% of the total mortality at age 0–0·5 years, but 95% of the plants dying at age 0·5–1·0 years were ramets. There was a remarkably constant annual death risk to mature plants within which was a seasonal cycle, April to October being the period of greatest mortality; a relatively risk-free flowering period separated two distinct peaks of mortality. The life expectancy of a plant arising from seed was

0·2–0·6 years but of a ramet was 1·2–2·1 years. The life expectancy of ramets appeared to be reduced at high density. In contrast *R. bulbosus* exhibited a low turnover rate and most of the deaths recorded were of plants less than 3 months old. The survivorship curve of established plants again contained a seasonal rhythm with two spring peaks. The population flux was greatest in *R. acris* and in some sites there was no permanent population, only a series of temporary but overlapping cohorts establishing from seed and soon dying. Mature populations again tended to have a constant annual survivorship curve with a seasonal rhythm.

The seasonal mortality risk was not synchronous in the three species and tended to occur when the pasture was in most active growth, not during the harsher climatic seasons. The death risk of seedlings tended to decline with age (Deevey type III) until after a few months it attained an annual constant value (Deevey type II) which differed from species to species.

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