Population Dynamics of the Grass Anthoxanthum Odoratum on a Zinc Mine

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POPULATION DYNAMICS OF THE GRASS *ANTHOXANTHUM ODORATUM* ON A ZINC MINE

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'Our knowledge about the lives of individual plants and of their persistence in plant communities is very incomplete especially when perennial herbs are concerned.' This remark made by Tamm (1948) is still largely true today: very few studies have been made on the longevity of plants in natural populations. Tamm (1948, 1956) mapped individual plants of various species over a 13-year period, using permanent quadrats. Harper (1967) re-analysed some of Tamm's data to show that the decay rates of the different species differed yet remained relatively constant over the period of the investigation. Sagar (1959, data quoted by Harper 1967) in a 2-year mapping study of *Plantago lanceolata* showed that this perennial herb in permanent grassland had a rapid population turnover. Harberd (1961, 1962) studying the clonal patterns in *Festuca rubra* and *F. ovina* concluded that there was probably very little population turnover and that some of the genotypes were likely to be over 1000 years old. Parallel studies on twelve other non-graminaceous species (Harberd 1962), on clover (Harberd 1963), and subsequent studies on grasses (Harberd 1967; Harberd & Owen 1969) showed the presence of more restricted clonal patterns. Williams (1970), in the only direct study of the longevity of perennial grasses, showed that *Danthonia cespitosa* had a relatively rapid decay rate (half-life of 15–30 months), which was somewhat decreased by grazing. *Chloris acicularis* behaved quite differently: under ungrazed conditions its decay rate was generally very slow (half-life of about 24 years) whereas under grazed conditions it was rapidly eliminated (half-life of about 2 months).

The present mapping study was undertaken between August 1964 and September 1970 to obtain data on the rate of population turnover and individual longevity in *Anthoxanthum odoratum* L., sweet vernal grass, on a derelict mine site.

STUDY AREA AND METHODS

The investigation was carried out at Trelogan Mine, Flintshire, Wales, U.K. (Nat. Grid reference: SJ 123805). The mine tip soil has a pH of 6·1–7·6, and contains 24 000–80 000 ppm zinc, 2500–3600 ppm lead, and 100–500 ppm copper. The first published returns from the mine were in 1848 and the mine was actively worked during the periods 1859–1873 and 1898–1909 with a period of sporadic reworking of old waste heaps between 1873 and 1898 (Smith 1921). The general topography and appearance of the area on which *Anthoxanthum odoratum* grows indicates that it is the part where the former tip had been reworked. The area under investigation was therefore almost certainly exposed for colonization between 1873 and 1898.

As well as *A. odoratum*, the mine is colonized by *Festuca ovina*, *Agrostis tenuis*, *A. stolonifera*, *A. tenuis* × *stolonifera* hybrids, *Minuartia verna* and *Rumex acetosa*. The areas of lesser contamination around the edges of the mine carry, in addition to the above, *Plantago lanceolata*, *Viola lutea* and *Euphrasia* sp. The degree of plant cover on the mine is very variable but in the study area it is in the order of 50%: the plants form an open community.

Plants of *Anthoxanthum odoratum* were mapped by marking their position on line transects: a plant was recorded as present if its vegetative tillers came directly below a tape measure. There were six transects, each 10 yd long (9·1 m), radiating out towards the mine centre from one point which was situated 5 yd (4·6 m) from the mine/pasture boundary. The site was about 20 m from the transect studied by McNeilly & Antonovics (1968), Antonovics (1968) and Antonovics & Bradshaw (1970), and generally located between their transect site positions 2 and 3. Recordings were made intermittently in 1964, 1965 and 1968, and more fully during 1966, 1967, 1969 and 1970. All individuals that were clearly identifiable as *A. odoratum* were mapped. This included seedlings at the 3–4 leaf stage.

The method employed for mapping the plants had the advantage of being rapid but suffered from inaccuracies on three main counts. Firstly, since the tape measure was often stretched over uneven ground, parallax errors could occur. Secondly, and related to the previous point, it was often a subjective decision as to whether a plant was situated 'directly below' the tape measure. Thirdly, since a line transect was used, death could not be distinguished from plant movement by lateral growth off the transect.

Several precautions were taken both in recording and in analysing the data to correct these deficiencies. Recordings made on successive dates were made independently. In analysing the data the following rules were adhered to: if the position along the transect of two successive recordings deviated by 1 in. (2·5 cm) or less, then this was attributed to error; if a plant was not recorded on one occasion, but was present in the same position (on the criterion outlined previously) prior to and following that occasion, then the record was taken to be continuous; if a plant was recorded on only one occasion it was classified as 'sporadic' and omitted from the major analysis. In this way, and if at any other point arbitrary decisions had to be made, the analysis was weighted towards *over-estimating* individual longevity. During the latter part of the study (1969 and 1970) independent replicate readings were taken at each visit and there was good agreement between replicates. An estimate of plant movement by lateral growth was obtained by studying the movement of the position of long-lived individuals along the transects. An analysis of the positions of individuals present at the start of 1966, and still present at the end of 1967 (i.e. over a 2-year period), showed that out of forty such individuals only four had a different position along the transect, and in only one of these cases was the deviation more than 1 in. (2·5 cm). *A. odoratum* does not appear to produce spreading tillers, and this was confirmed by the mapping data.

The mapping had to be terminated since a major part of the study area was destroyed by the laying of a water main.

RESULTS

(a) *Population density*

The total number of plants recorded on the transects (Fig. 1) showed both seasonal and long-term fluctuations. In general, population density increased in spring, reached a peak in July and declined in the late summer and early autumn. The seasonal increase probably represents favourable conditions for germination, for growth of previously germinated seedlings or, since *Anthoxanthum odoratum* is early flowering (Table 1), recruitment from

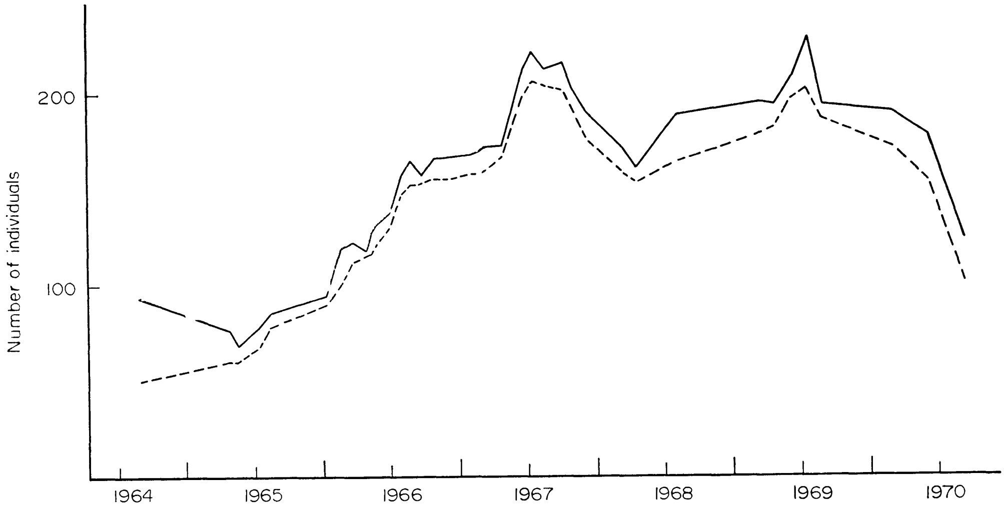

FIG. 1. Total number of plants recorded on the transects during the study period. Changes in plant number are an indication of relative changes in population density. ——, Total population including plants recorded only once; – – –, plants recorded on more than one occasion.

Table 1. *Flowering time of* Anthoxanthum odoratum *at Trelogan mine*

Percentage of plants with at least stigmas exposed	Date
86	15 May 1964
48	12 May 1965
83	23 May 1966

FIG. 2. Age distribution of plants at different times during the study period. (The ages of the older plants during the early part of the investigation could not be determined since their date of establishment was not known.) ——, Half-year intervals; – – –, 1-year intervals as indicated.

the current year's seed crop. In the whole study only nineteen new individuals could be traced to the 'branching' of a pre-existing individual. Recruitment and spread by vegetative propagation appeared to be relatively unimportant.

Over the whole study period the population density appeared to show an initial decrease, followed by a general increase from 1965 to 1967, and a decline in 1970. Clearly the study was not carried on for long enough to determine whether these long term changes represented regular or irregular fluctuations.

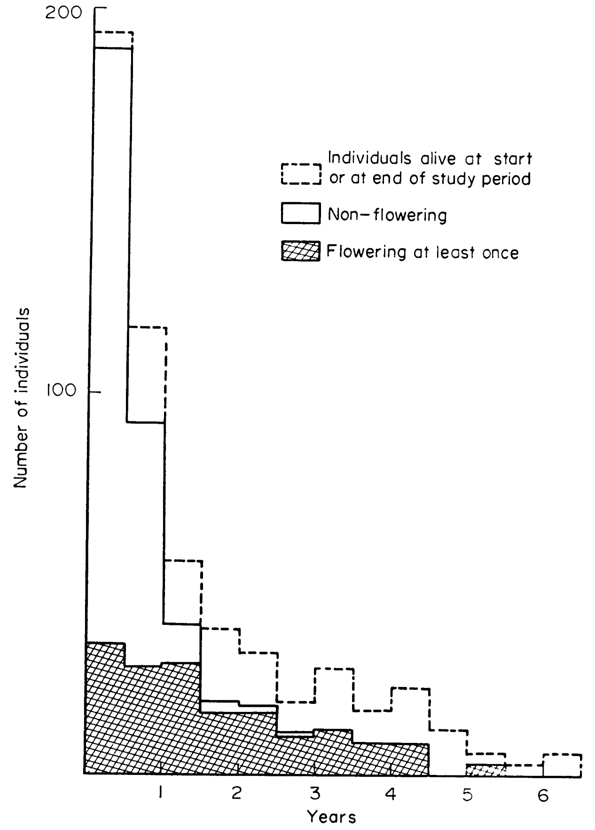

FIG. 3. Overall individual longevity of plants.

(b) *Age distribution*

There were marked shifts in the age distribution of the plants during the study period (Fig. 2). For example, during the period of rapid population increase in 1966 nearly 75% of the population was composed of individuals less than 1 year old, whereas following the drop in population density in 1970, only 12% of the population were less than 1 year old. The shifts in age distribution could be seen to reflect the previous history of the population (cf. Kerster 1968). For example the high percentage (*c.* 25%) of individuals between 2 and 3 years towards the end of 1968 reflected the high rate of recruitment in 1965 and 1966.

(c) *Individual longevity*

Measurements of individual longevity showed that only a small fraction of the individuals lived for more than a few years (Fig. 3). Out of a total of 546 individuals recorded

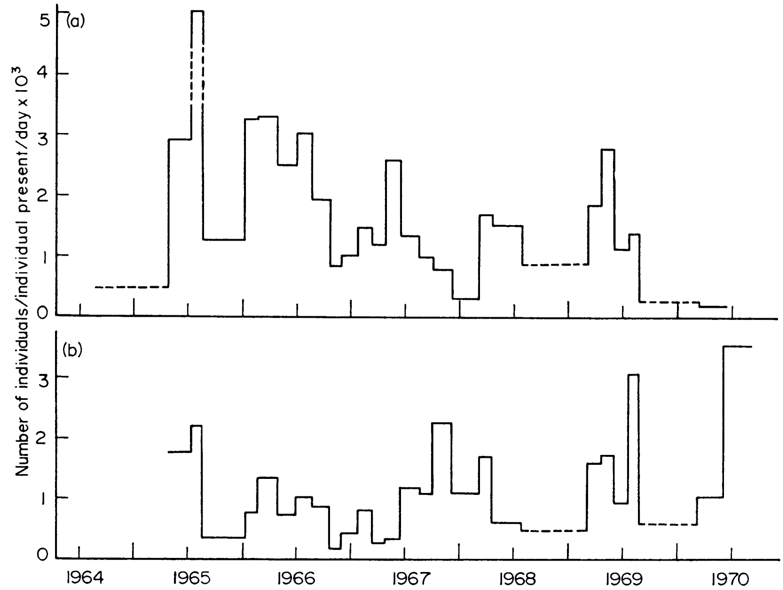

FIG. 4. The relative recruitment (a) and mortality (b) rate for individuals living more than 120 days for intervals greater than 30 days during the study period, measured as number of recruitments or deaths per individual present prior to recruitment or death per day × 10^3. (Pecked lines indicate intervals where the rates may have been slightly under-estimated.)

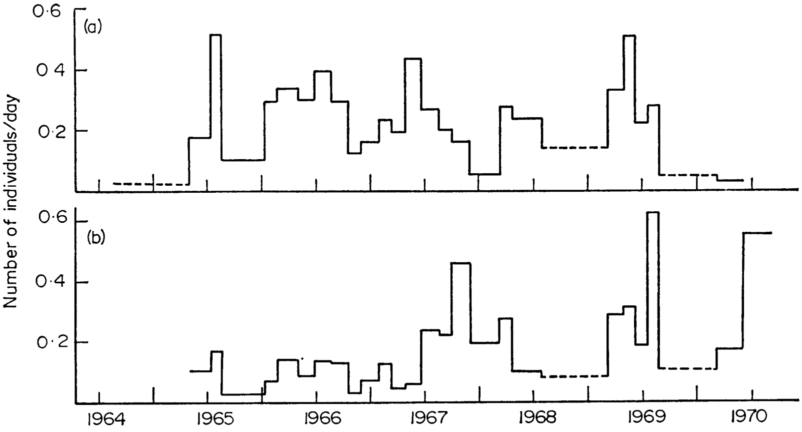

FIG. 5. The absolute recruitment (a) and mortality (b) rate for individuals living more than 120 days for intervals greater than 30 days during the study period, measured as number of recruitments or deaths per day. (Pecked lines indicate intervals where the rates may have been slightly under-estimated.)

(excluding single 'sporadic' records) only sixteen lived for more than 5 years. A large proportion of the short-lived individuals failed to flower, whereas all the individuals living 3 or more years flowered at some time during their life time. Population maintenance appeared to be a very dynamic process.

Generally plants with a greater life span achieved a larger size, but their size did not progressively increase during their life time. For example the six individuals that persisted throughout the study period showed a slight non-significant decrease in mean diameter. They differed considerably in size and maintained this size difference during the study period. Similar results were obtained by Tamm (1956). Individuals towards the end of their life span often showed reduced size. The relationship between plant size and longevity is therefore very tenuous.

(d) *Recruitment and mortality rates*

The relative recruitment and mortality rates (number of recruitments or deaths per day per individual present prior to recruitment or death) and absolute recruitment and mortality rates (number of recruitments or deaths per day) have been plotted in Figs. 4 and 5, respectively for time intervals greater than 30 days, and for individuals living more than 120 days. Only those individuals living more than 120 days have been included since in general the time interval between successive readings was shorter than this and therefore the data are not biased by an unknown number of individuals recruited and dying between successive readings. Where the time interval between two successive readings is greater than 120 days (pecked lines in Figs. 4 and 5) the rates may be under-estimated. Relative recruitment rates were generally high and mortality rates low at the start of the study period, whereas the converse tends to be true towards the end of the period. The absolute recruitment rate tends to fluctuate about a fairly constant level whereas the absolute mortality rate increases towards the end of the period. Seasonal trends are very apparent. Recruitment is generally low in the winter months, high in the summer but reaching a peak at different times in different seasons. Recruitment even in the winter months is never zero; this is possibly a reflection of the mild climate of the region. For example, over the 5-year period between 1964 and 1968 the lowest monthly mean minimum temperature was −0·2° C and the highest monthly mean maximum temperature was 20·0° C; the highest total monthly rain was 5·68 in. (144·3 mm), the lowest 0·28 in. (7·1 mm) (records for Prestatyn, *c.* 3 miles (4·8 km) from Trelogan; Meteorological Office, London). Mortality rates show similar seasonal fluctuations being low in the winter (except for the winter of 1967–1968) and high in the summer. There is no significant correlation either between relative recruitment and mortality rates ($r=0{\cdot}366$, $P=5$–10%), or between absolute recruitment and mortality rates ($r=0{\cdot}162$, $P>10\%$). However, in terms of the shift between successive time intervals, the changes in recruitment rate and

Table 2. *Changes in recruitment and death rate over successive time intervals*

Relative recruitment and death rate

		RECRUITMENT	
		Increase	Decrease
MORTALITY	Increase	11	3
	Decrease	0	11

Exact two-tail probability, $P=0{\cdot}012\%$

Absolute recruitment and death rate

		RECRUITMENT	
		Increase	Decrease
MORTALITY	Increase	10	3
	Decrease	3	9

Exact two-tail probability, $P=1{\cdot}69\%$

mortality rate parallel each other closely: an increase or decrease in recruitment rate is accompanied by a corresponding shift in mortality rate. This correspondence is statistically significant (Table 2).

The association between mortality and recruitment may be because they are both affected in parallel ways by the environment. Attempts to correlate the changes in birth and death rates with climatic conditions as recorded for Prestatyn, 3 miles (4·8 km) away (mean maximum and minimum temperatures, hours of sunshine and rainfall), failed to produce any trends which could not be attributed to the seasonality of the recruitment and death rates. The low winter death rates are perhaps surprising in view of the ostensibly harsher climatic conditions, but during the summer the plants may succumb to metal toxicity. The most likely causes of summer death are drought and the consequent concentration of metals by upward water movement and evaporation in the surface layers of the soil. Since high metal concentrations interfere with internal cell metabolism (Turner & Gregory 1967; Peterson 1969) perhaps the plants are more susceptible to toxicity when they are actively metabolizing. A severe drought in the summer of 1970 may have been the reason for the drop in population number at the end of the study period. In view of the dynamic nature of the population it is possible that factors increasing mortality and recruitment may be successively present over fairly short time intervals during the summer period. It is almost certain that more frequent and accurate estimates of recruitment and mortality rates would have to be made to obtain a significant correlation with environmental factors.

Alternatively one can postulate a causative relationship between mortality and recruitment rates: recruitment of new individuals may increase the probability of death of existing individuals (i.e. mortality is density dependent) or mortality of existing individuals may facilitate recruitment of new individuals. However, it is difficult to decide which, if either, of the alternatives is valid. For example, as population size increases through to mid-1967, the relative mortality rate decreases, but is then abnormally high in the following winter. This high mortality rate is followed by an increase in recruitment, but in the following season as population size increases both mortality and recruitment are high.

The factors controlling recruitment and mortality rates are clearly complex and cannot be unravelled by such purely descriptive data.

(e) *Population decay rates*

The decline in numbers of plants present at the beginning of successive years of the study was plotted on a natural log scale and regression lines fitted. When the whole population is considered (Fig. 6), i.e. individuals starting in one year are included with those established in previous years, the rate of population decay remains more or less constant over time. Moreover, since the regressions do not differ significantly in slope ($P = 19\%$) the decay rate is constant irrespective both of the initial population size, and of the time period studied. The overall regression gives a population half-life of 2·05 years (i.e. 71·3% of the population present in one year survive to the next).

When the course of population decay is plotted for the new arrivals in each year (Fig. 7), they too have a constant decay rate. However, the slopes of the regression lines are significantly different ($P < 0{\cdot}1\%$), indicating the segments of the populations recruited at different times have different decay rates. These vary from a half-life of 2·17 years for the population recruited during 1966 to a half-life of 0·95 years for the population recruited during 1968. The overall regression gives a population half-life of 1·98 years (i.e. 70·5%

of the population present in one year survive to the next), a figure close to the one obtained for the total population on successive years.

Short-term fluctuations in decay rates are evident but, in general, decline of the populations is not due to sudden castastrophic events. These short-term changes usually represent the seasonal fluctuation in mortality rates discussed earlier. Towards the end of the study period, where there is a rapid decline in the population, it can be seen from Fig. 7 that this decline is largely accounted for by an increase in the decay rates of populations recruited during 1966 and 1968; the decay rates of the other populations remain relatively constant. The 1966 and 1968 populations differ markedly in their age distribution yet react in similar ways. The individuals recruited in 1966 and 1968 may have been genetically unsuited to the conditions in 1969 and 1970 or they could have been unsuited

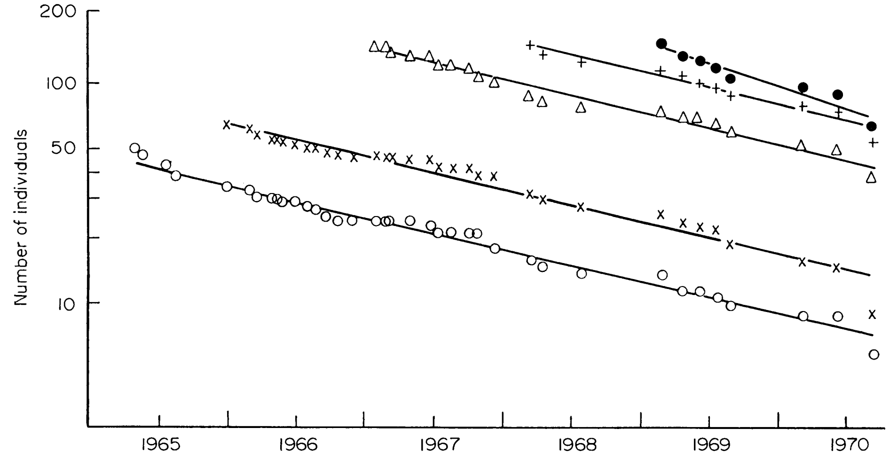

FIG. 6. The decay rate of the population present at the beginning of successive years of the study period. Ordinate on log scale.

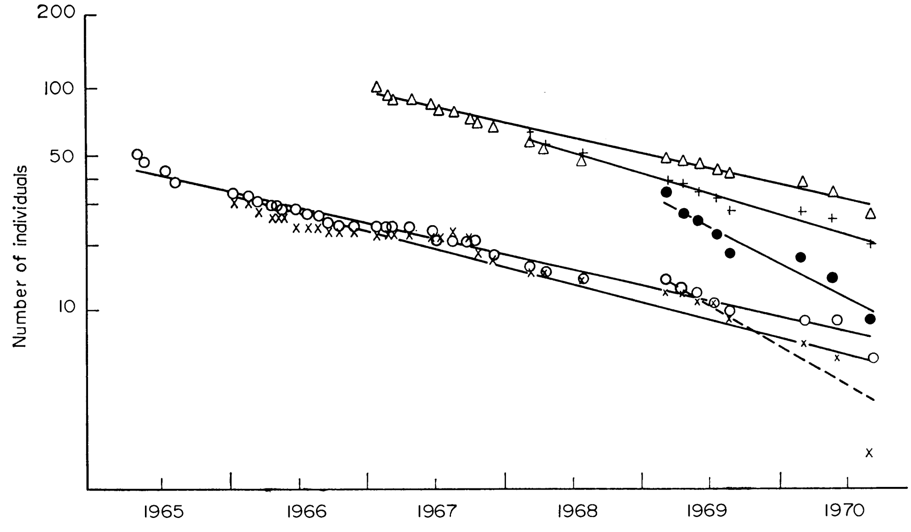

FIG. 7. The decay rate of the population of plants establishing in the previous year for successive years of the study period. The plot for 1965 onwards includes individuals established prior to the whole of the study period. (The pecked line is a regression fitted to the 1969 and 1970 points of the plot for 1966 onwards.) Ordinate on log scale.

Table 3. *Distribution of individual longevity in the different transects*

Transect no.	Years $<\frac{1}{2}$	<1	$<1\frac{1}{2}$	<3	<4	>4
1	29	15	3	15	8	12
2	42	27	14	5	6	6
3	21	13	8	11	7	15
4	37	21	11	11	8	13
5	38	26	10	13	11	8
6	25	15	10	11	7	14

Heterogeneity $\chi^2_{25}=30{\cdot}95$, $P<25\%$.

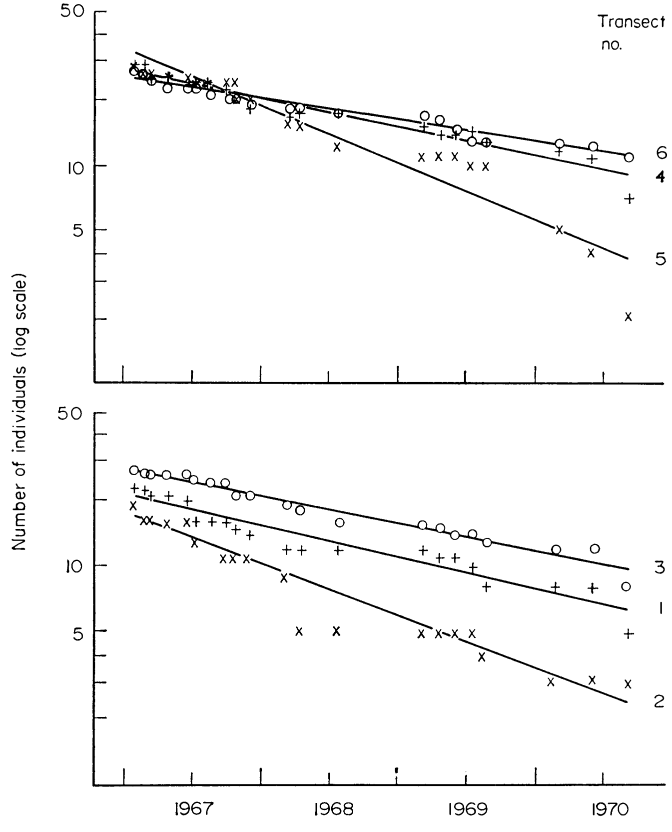

FIG. 8. The decay rate of plants established in 1966 for the six transects.

by common environmental influences operating during their establishment (e.g. wetness encouraging shallow roots).

(f) *Differences between transects*

In 1969 and 1970 replicate readings were taken on each visit. An analysis of variance on the number of plants recorded gave highly significant ($P<0{\cdot}1\%$) differences between transects, between times that the readings were taken, and interaction between times and transects. The changes recorded in the population are therefore significant, the transects differ in plant density, and the numbers of plants on different transects are different at different times: the fluctuations in population density are not the same in all transects.

The transects did not differ significantly in terms of the distribution of individual longevity (Table 3).

The decay rate of plants from each transect established in 1966 is shown in Fig. 8. The slopes of the regression lines are significantly different ($P<0\cdot1\%$) giving variations in half-life from 1·18 years to 3·11 years, and an overall half-life of 1·85 years (i.e. 68·7% of the population present in one year survive to the next).

These differences between the transects are undoubtedly a reflection of the heterogeneity of the mine tip area (cf. Antonovics & Bradshaw 1970).

DISCUSSION

The population of *Anthoxanthum odoratum* growing on the waste tip of the zinc mine at Trelogan has a rapid turnover. Only a minute fraction of the population lives for more than 5 years, and the population half-life is in the order of 2 years. Population maintenance must be a dynamic process in this perennial grass. It indicates that selection must be proceeding continuously and actively to maintain the differences between these mine plants and their counterparts a few yards (metres) away on normal pasture (McNeilly & Antonovics 1968; Antonovics 1968; Antonovics & Bradshaw 1970; Antonovics, Bradshaw & Turner 1971).

This rapid turnover may be a reflection of the harsh mine conditions, and turnover of the same species in pasture may be far slower. However, other perennial herbs in pasture conditions do show rapid turnover (Harper 1967; Williams 1970), and perhaps the changes in genetic composition of grasses sown in permanent pasture (e.g. Charles 1964; Crossley & Bradshaw 1968) reflect not just differential mortality of existing types, but actual replacement.

If the dates of recruitment and of death of individual plants are known it appears at first sight possible to construct life tables for this population on the basis of either (a) age at death, (b) number of survivors over time out of an initial number, or (c) age structure of the population (Deevey 1947; Harcourt 1969). However, the varying age structure of the population precludes the use of age structure itself as the basis for life table construction and furthermore invalidates the use of overall plant longevity (Fig. 3) as a generalized survivorship curve for the population. Unfortunately the number of individuals becoming established between any two particular recording dates were too small to produce accurate survivorship curves based on the decline in number of survivors over time. However, if the arrivals for the previous year are pooled, then Fig. 7, showing the decay rates for newly arrived individuals over successive years, is formally equivalent to survivorship curves.

It can be seen that the survivorship curves are highly consistent with Type II of Deevey (1947) or Type III of Slobodkin (1962) indicating constant mortality risk with time. These survivorship curves clearly do not include seed and seedling mortality. In view of the large numbers of seed produced, absence of innate (constitutive) dormancy, and the observed mortality at the seedling stage when non-tolerant seed is sown on toxic soil (McNeilly 1968; Bradshaw *et al.* 1969), it is likely that the mortality rate in the juvenile stages is far higher. The overall survivorship curve is therefore almost certain to approximate to Type III of Deevey (1947) or Type IV of Slobodkin (1962) although its precise pattern in the early stages remains undefined.

In the present study mortality has been largely described in terms of population decay rate. This parameter integrates the causes of mortality over different ages, different times of establishment, different dates, and different locations in the habitat. There were significant differences between all these components of the overall population decay rate, but the overall decay rate itself did not change significantly over a 5-year period. Williams (1970) also showed differences in decay rate depending on age of the individuals, different times of establishment, and different environments (grazing regimes). This apparent conflict between his data and the conclusions of Harper (1967) led Williams to state that 'steady decay in populations reflects an environmental regime that is consistently favourable, or unfavourable.'

The present study indicates that population decay rates are like any phenetic characteristics, and that there is no basic conflict in the views of Harper (1967) and Williams (1970). Mortality can be studied at several levels and with a view to answering different questions: it is likely to vary between individuals, populations and species and to be affected by the environment and genotype. The detailed shifts in mortality may lead one to inquire into its specific causes, whereas the overall pattern will lead one to ask about life history strategy. The data of Williams (1970) show that generalizations similar to those made by Harper (1967) about decay rates are possible: decay rates *do* tend to remain linear when considered over long periods of time and are species and environment specific.

The significance of life tables and survivorship curves has been elegantly discussed by Deevey (1947), particularly with regard to the dilemma of the apparently more or less fixed life-span of species ('physiological life table' or 'endogenous senescence') and their naturally observed life span ('ecological life table' or 'exogenous senescence'). This relates to the question of whether the pattern of mortality is environmentally or genetically determined, and one can raise a similar question with regard to population decay rates. Deevey (1947) succinctly states that 'we can not observe physiological survivorship except in an environment of some sort', and it is almost certain that a population can adjust its decay rate (and its components) by evolutionary change. Equally, of course, environmental shifts can cause changes in the decay rate which may or may not be followed by evolutionary response; environmental effects are clearly seen in the present study and in the work of Williams (1970).

There is evidence from crop plants that longevity is easily changed by selection, in the direction of both increased and decreased longevity (e.g. Helbaek 1959; Hutchinson 1962; Khush 1962; Schwanitz 1966; Oka & Morishima 1967). *A. odoratum* itself appears to have populations differing considerably in their longevity. For example in Britain, Clapham, Tutin & Warburg (1962) describe the plant as 'perennial', whereas in the south-eastern United States the plant is described as 'perennial or winter-annual' (Radford, Ahles & Bell 1964). Variations in longevity of different populations of *A. odoratum* grown under cultivation have also been observed (A. D. Bradshaw, unpublished; Böcher 1961). Böcher (1961) found that out of twenty-seven populations (ten–fifteen plants per population) from various localities in Europe, one population behaved as a biennial, seven populations survived for 3 years, in three populations only some individuals survived for more than 3 years, whereas in the remainder all the plants lived for more than 3 years. In general short-lived populations tended to flower in their first year and be characteristic of lowland as opposed to montane localities. Less marked differences in longevity of different populations under cultivation have been observed in *Dactylis glomerata* (Böcher 1961) and *Holcus lanatus* (Böcher & Larsen 1958) with southern populations tending to be shorter lived than more northerly ones.

The reasons for genetic differences in longevity, which in natural populations of herbaceous perennials may express themselves as differences in decay rates, are undoubtedly complex.

Differences in longevity may be related more or less directly to the environment. For example, clear-cut periodic environmental hazards which do not permit the survival of adults may select for short-lived individuals (e.g. in desert ephemerals or Mediterranean winter annuals), or the low energy environments of arctic and alpine regions may favour a long-lived perennial habit since energy for reproduction is more efficiently obtained by a mature individual than by regular re-establishment from the seedling stage (Billings & Mooney 1968). Only in alpine regions of relatively high light intensity and temperature, as in the Sierra Nevada of California, is there an appreciable number of annuals (Chabot 1971). The general trend towards increasing longevity of grass ecotypes in more northerly and montane regions observed by Böcher (1961) and Böcher & Larsen (1958) may be related to this. A greater relative contribution to vegetative parts (and therefore possibly reduced mortality risk) has been observed in low energy environments by Johnson & Cook (1968) and Harris (1970).

Population and species differences in individual longevity may be related to life history strategies: longevity is but one component of the life history and inter-relates with other components in complex ways. The subject has received considerable attention elsewhere (e.g. Cole 1954; Murphy 1968; Gadgil & Bossert 1970) and no attempt will be made to review the subject. The pattern of mortality is an obviously important component of such life histories. For example, Gadgil & Bossert (1970) consider the situation where, given a certain level of probability of death and a certain level of resource utilization (i.e. a constant environment), a change in the death rate will not affect the reproductive effort (amount of available resources devoted to reproductive effort) provided that the change does not affect the different stages in the life history in a different manner. Changes in a constant decay rate of the population meet the latter proviso (although it is not known what happens at the seed and seedling state) and it can be predicted that populations with considerably different decay rates may devote a similar proportion of their energy to reproduction.

A third way in which population decay rates might be important is in the genetic adjustment to a varying and unpredictable environment. If it is assumed that selection acts mainly in the seedling stage (see Barber 1965, for full discussion of selection at juvenile stages in plants) then the adults essentially provide the population with a 'memory' of past selective events and thereby conserve variability. If the memory is too long (i.e. decay rate and turnover is slow) then the population will tend to have an increased genetic load (selection intensity) since the present environment may have changed yet the gene pool and hence newly establishing individuals may be receiving contributions from genotypes that were favoured at an earlier date. On the other hand, if the memory is too short then genetic variability which can be used, should a particular environmental extreme recur, will not be available. An analogous memory system based on the perennial habit and dormant seed has been considered in a different context by Kerster & Levin (1970) and Harper (1957, 1959); long-lived individuals represent directly the population selected in the year in which they were established, whereas dormant seed represents the population before selection. Suggestive evidence for the existence of such memory systems may be seen in the current study where it was noted that individuals established during 1966 and 1968 showed an increased mortality in 1969 and 1970.

Moreover, individuals established in different years have different decay rates (cf.

Williams 1970), suggesting that in some years, during seedling establishment, there may be selection for characters increasing adult survival, whereas in other years there may be selection for characters which reduce adult survival.

It is clear that to establish acceptable generalizations further data are needed (particularly of a comparative nature between closely related species or ecotypes) on age to maturity, the variation of reproductive effort with age, fate of the seed, and subsequent survivorship of seedlings and adults in natural plant populations. The present data pertain mostly to the pattern of mortality in the established population and no attempt has been made to speculate on the precise causes of mortality. These are likely to be extremely difficult to define in natural populations: it is salutary to think of the difficulty of establishing the causes of mortality in as well studied an organism as man. Nevertheless the overall pattern of mortality is likely to be highly relevant to the ecology of an organism, subject to change by selection, and to influence the genetic architecture of the population. It is difficult to understand why its study has been so neglected by plant ecologists.

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SUMMARY

Individuals of *Anthoxanthum odoratum* L., sweet vernal grass, growing on zinc-contaminated mine waste were mapped over a 6-year period using a line transect method. The population density generally increased in the summer months, but otherwise fluctuated erratically during the study period. There were concomitant shifts in the age distribution of the population. Recruitment was mainly by seed. There was a positive association between recruitment and mortality rates, both being low in the winter months. Only a small fraction of the individuals lived for more than 5 years, the half-life of the population being in the order of 2 years. The overall population decay rate of individuals present in the previous year did not differ significantly with time and/or with population density. However, individuals established in different years and individuals from different transects showed significant differences in decay rates. These results showed that there was rapid population turnover and therefore strong selection acting to maintain the characteristics of the mine population. Population decay rate was considered to be influenced both by the environment and genotype, and the ecological and genetic significance of longevity was discussed.

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