Studies in the population dynamics of some Teesdale plants

Doody, J. P.

STUDIES IN THE POPULATION DYNAMICS OF SOME TEESDALE PLANTS

being a

Thesis for the Degree of
Doctor of Philosophy
of the
University of Durham

by

J. P. DOODY, B.Sc.(Sussex)

October 1975

The early part of this work, including the establishment of sites, was carried out by Miss M. Watson during 1968. In 1969 recording was continued by J. Muggleton and Dr. M. E. Bradshaw. The study reported here includes the data collected during this period, Autumn 1968 to Autumn 1969.

ABSTRACT

The study was essentially a demographic one. Few studies of this kind have been carried out on rare plant populations.

Permanent quadrats (selected subjectively for the presence of some Teesdale plants, including Gentiana verna and Polygala amarella) were established on Widdybank and Cronkley Fells in the Northern Pennines. The quadrats were all established on the grazed or eroding areas of sugar limestone grassland. For each quadrat the grid positions of all the individuals of the species being recorded were plotted on a chart. The fate of the initially recorded mixed-age population and that of all subsequent additions was noted at each visit.

Larger permanently marked sample sites, usually adjacent to a permanent quadrat, were recorded once a year for the number of flowering and non-flowering individuals. Individuals which flowered were then recorded for the number of flowers, fruits and seeds they produced.

From these data the population flux, mortality, survival and age-distribution of the individuals in the quadrats were obtained. The relative importance of sexual reproduction was ascertained by closely following the appearance of seedlings and vegetative shoots in each of the quadrats where a species produced both.

ACKNOWLEDGEMENTS

I am grateful to the Teesdale Trust who provided the funds which enabled this work to be carried out, and to Dr. Margaret Bradshaw whose supervision of the project and help in the production of this thesis was invaluable. I should also like to thank Professor Boulter who made available laboratory facilities, Mr. Tom Baffey for his assistance and hospitality and the staff of the Nature Conservancy in Teesdale, particularly Dr. T. J. Bines for his help and advice.

My thanks also go to Miss V. Cairns who typed the thesis. Finally, I am particularly indebted to my wife for her help in producing the diagrams and forbearance during the latter stages of the production of the thesis.

CONTENTS

CHAPTER FIVE: VIOLA RIVINIANA

CHAPTER SIX: VIOLA RUPESTRIS X RIVINIANA

CHAPTER SEVEN: POLYGALA AMARELLA

CHAPTER EIGHT: DRABA INCANA

CHAPTER NINE: GENTIANA VERNA

CHAPTER ONE

INTRODUCTION

PLANT POPULATION STUDIES

Population dynamics has long been the prerogative of zoologists and studies on plant populations have been relatively few. The study of animal populations was stimulated by the need to explain the evolutionary mechanism controlling the rate at which, theoretically at least, a population could expand. Darwin (1859), stated, 'Every being which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life . . ., otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product'. In addition, and perhaps of greater significance, was the need to understand the often large scale fluctuations in many pest species, Andrewartha (1961). In this context the innate capacity for increase was a concept of considerable importance, Andrewartha and Birch (1954). This is an estimate of the potential for population growth given that there are no environmental constraints such as climate, growth medium, interspecific or intraspecific competition.

In plant populations this concept has been applied relatively infrequently, although the reproductive ability of some annual species, capable of producing very large numbers of seeds, might have stimulated more work, similar to that carried out by zoologists. Selman (1970), showed that the estimation of annual weed populations and their reproductive potential, in terms of the number of spikelets which were produced, can provide sufficient information on how plant numbers change from year to year.

There are perhaps two properties of plants which have to some extent hindered the study of plant population dynamics, plasticity and vegetative reproduction. Clearly when clones of vegetative shoots are produced which may be centuries old, Harberd (1962) and (1963), the definition of the individual becomes a problem. However, population studies can be made if the daughter shoots, 'ramets' of Kay and Harper (1974), are treated as individuals in a population.

The majority of studies on plant populations have been carried out on perennial herbaceous plants, mostly occurring in grassland communities. In these habitats many of the species reproduce wholly or partially by means of the production of vegetative shoots. The results obtained indicate that studies of this kind can be very revealing.

In one of the best known attempts to record changes in naturally occurring populations, Tamm (1948) and (1956b), followed the behaviour of a number of plant species in permanent quadrats situated under a spruce canopy and in a meadow. For the species studied, including Centaurea jacea, Filipendula vulgaris and Anemone hepatica, individual plants were charted within permanently marked sample plots. The fate of the individuals, whether they flowered or died, was followed and new individuals noted. Tamm (1956b) in discussing the results for the 13 years between 1943 and 1956 remarked on the stability of the populations and corresponding low rate of mortality and recruitment. More recently, Tamm (1972a), reported the results for a longer period of between 14 and 30 years for several species of orchid, and from 1943 to 1971 for Primula veris, Tamm (1972b). These last two studies give important information on the changes in plant populations over a relatively long period of time. For example in the case of 4 of the orchid species it was clear that their numbers decreased over the study period. This appeared to be due to the fact that although propagation by seedlings did occur, the recruitment rate of new individuals to the populations was very slow in the closed plant communities in which the plants occurred.

Tamm's early data was recalculated by Harper (1967) and presented as the logarithmic change in plant numbers with time. He remarked on the linear nature of the relationship, showing loss of individuals from the population as a slow, steady process which could be characterised, like the decay of a radioisotope, by a 'half-life'. This parameter used as an indication of the rate of turnover of individuals gives an important insight into the dynamic nature of plant populations. The values given for Centaurea jacea, Filipendula vulgaris and Sanicula europaea of c. 1.9, c. 18.4 and 50 years respectively in the paper indicate how much variation there can be in the rate of change in the populations of different plant species.

The half-life values can be particularly revealing for perennial species, although problems can arise when species reproduce by the production of seed which has a high risk of mortality during the early stages of establishment following seed germination. In these cases, either the groups of individuals with the higher risk of mortality should be omitted from the figures used in the calculation of 'half-life' or a modified equation should be used. The values quoted in the literature have been calculated using the decay of a mixed-age population. These populations usually do not include seedlings and the evidence presented below indicates that their rate of decay is constant and a function of the number of individuals only. In these circumstances the formula for the decay of a radio-active isotope gives a fairly accurate assessment of the half-life of the plant populations.

Antonovics (1972) calculated half-life values for mixed populations of *Anthoxanthum odoratum* which included individuals starting in one year with those established in previous years. A value of 2.05 years was obtained for this group of plants, whilst half-life values for the new arrivals (seedlings) in each year varied from 2.17 for the population recruited during 1966, to 0.95 for the population recruited in 1968. These figures give an indication of the very rapid rate of turnover in this population, both of mature plants and seedlings. (Both the mixed-age populations and the populations of seedlings indicated that the rate of decay remained more or less constant with time).

By contrast, the half-life values calculated from Tamm's data, Harper (1967), for *Filipendula vulgaris* and *Sanicula europaea* quoted above indicate a very slow rate of turnover. For these species this is associated with high individual longevity, and a correspondingly slow rate of replacement by the production of new vegetative shoots and occasional seedlings. Under these circumstances the population at any one time consists of a high proportion of mature individuals and very few new recruits.

These studies illustrate two strikingly different life-history strategies, repeating producers and the 'big bang' producers of Gadgill and Bossert (1970). The first of these strategies is restricted to perennial plants whilst the second is employed by annuals and biennials and may also be used either instead of, or in conjunction with, vegetative reproduction in perennials. Apart from the records of the changes in the numbers of some annual weed populations of agronomic interest such as *Avena fatua*, Selman (1970), other data on population regulation of both annuals and biennials are almost non-existent. The most complete plant investigations have been carried out on perennial species which are components of grassland communities.

Since the early studies of Tamm these species have been shown to have a variety of life strategies, sometimes with marked differences between closely related species. For example, Sagar (1959), studied *Plantago lanceolata*, *Plantago major* and *Plantago media* using pantographic techniques, in permanent grassland under three management regimes. He found the most stable population was *Plantago lanceolata* growing in poor grassland which was lightly-grazed during part of the year with a mid-Summer hay cut. Under a second management regime there was an overall decline in the populations of *Plantago lanceolata* and *Plantago media* in an area grazed in 3 out of 4 years with hay cut in the fourth year. This decline was attributed to the lack of seedling establishment. In the third site the grassland, which was part of a large garden, suffered periodic flooding and was cut with a scythe. Under these conditions *Plantago major* was common with occasional *Plantago lanceolata*. However, when cutting was stopped and the herbage grew freely the former species was eliminated from the sward. A subsequent flooding produced large numbers of *Plantago major* seedlings after desolation in the areas and there was a total loss of *Plantago lanceolata* from the area. Clearly each of these species was affected in a different way by different environmental factors and their survival required particular conditions which allowed the germination and establishment of seedlings.

This type of study can lead to an understanding of the way environmental factors operate by controlling the rate of establishment of new individuals, and so determine the spatial distribution of the species. Perhaps the most revealing study of this kind is that of Sarukhan and Harper (1973), who examined three species of buttercup, *Ranunculus repens*, *Ranunculus bulbosus* and *Ranunculus acris*. They considered the species to be ideal for comparative demographic study because they are (1) closely related, (2) common, (3) live in the same area within an extensive and stable ecosystem, and (4) represent different life-strategies.

The three species were examined in an area of former ridge and furrow grasslands established on arable lands, Harper and Sagar (1953). They found that the species were ecologically restricted and one factor probably responsible for the zonation was the different requirement for seed germination and establishment. *Ranunculus repens* occupied the bottom of the furrow which was poorly drained and often water-logged, but seedlings of this species were able to establish very successfully under these conditions. *Ranunculus bulbosus* grew along the drier ridges and it was in this situation that seedling establishment for the species was most effective. *Ranunculus acris*, which occupied an intermediate position between the two other species, also had intermediate requirements for successful seedling establishment.

As well as recording the changes in the numbers of individuals, that is, population flux, survivorship and mortality, Sarukhan (1974) related the contribution of seed production and the dynamics of the buried seed to the replenishment of the population. *Ranunculus repens* with a dependable vegetative reproduction, had weak flowering and therefore low seed production. However, this was compensated for by the fact that the seed survived for a long time in the soil. This 'reproductive strategy' contrasted strikingly with the other two species which had little or no vegetative reproduction, high seed output, rapid germination and short life of buried seed.

Putwain (1970) and Putwain and Harper (1970) studied populations of *Rumex acetosa* and *Rumex acetosella* in grasslands in North Wales and an attempt was made to determine the mechanism of population regulation at different stages in their life cycles. They found that most populations of *Rumex acetosella* were controlled by a plastic reduction in the ability of the species to reproduce vegetatively at high densities. *Rumex acetosa*, on the other hand, is regulated at the germination and establishment phase of its life cycle. For both species seedling establishment is very difficult in closed grassland communities and new individuals arising from the mode of reproduction require local disturbances of the sward to allow germination and establishment. Once established, however, both can reproduce vegetatively and thus are able to survive in a closed sward, although *Rumex acetosella* is often more typically found in disturbed habitats such as burnt areas of moorland.

Environmental factors not only operate through the control of the different stages of the life-cycle, as outlined above, but may also determine the form of the life-cycle itself. This was clearly illustrated for *Trifolium pratense*, by Rabotnov (1960) quoted in Harper and White (1970), who examined its growth in both floodplain meadows and sub-alpine meadows. In the first of these situations the number of clover plants fluctuated a great deal; the plants usually flowered once within two years of seedling establishment and then died. A new population was formed by seedling establishment and there was a rapid turnover of the population as a result of the 'big bang' method of reproduction.

By contrast, red clover in the sub-alpine meadows became polycarpic. Plants did not flower until they were 5 to 10 years old; thereafter they flowered either every year or once every 2 or 3 years, some individuals reaching 20 years of age. The rate of population turnover in this second situation was much slower. This was reflected by the low seed yield and slow rate of replacement of individuals.

The above studies were largely concerned with the way in which plant populations were regulated. In the words of Darwin (1859), 'Look at a plant in the midst of its range, why does it not double or quadruple its number?' However, the reverse of this must also be considered, 'Why does a species survive?' Clearly, this has a direct bearing on rare plant populations, in particular, where the main question to be answered is, how does the population ensure there are sufficient new plants to maintain its numbers?

Perennial herbs, which make up approximately 90% of grasslands in temperate regions, often have the ability to reproduce both by means of the production of vegetative propagules and seed. Under grazed conditions and in a closed sward the second mode of reproduction is often curtailed and survival of the species is facilitated in the short term by the ability of the plants to produce vegetative shoots. Clearly sexual reproduction may be important to the long term survival of the population, allowing adaptation to changing environmental conditions.

Bliss (1962) discussed the adaptations of arctic and alpine plants to adverse environmental conditions and many of these are applicable to species growing in Upper Teesdale. For example self-pollination is often more important than wind and insects, although bumble bees seem to be of some importance. In Teesdale, *Viola rupestris*~~,~~ and *Viola riviniana* (Chapters four and five) both have cleistogamous flowers which produce relatively large numbers of seed and *Draba incana*, (Chapter eight) and *Polygala amarella* (Chapter seven) are predominantly inbreeding species, Fearn (1971). Many plants of the tundra are reduced in size so that the aerial parts are in the more favourable lower part of the micro-environment where higher temperatures prevail.

Bliss also indicated that many species produce viable seed whilst others do not and suggested that in some years large numbers of seed germinate and become established. In Upper Teesdale a large proportion of the species can produce seed but many, for example, *Primula farinosa*, *Tofieldia pusilla* and *Gentiana verna* do so infrequently because the flowers are eaten by sheep. Other species produce little or no seed because few flowers are produced. For example during the four years of this study only one flower of *Potentilla crantzii* was observed on Widdybank Fell.

Another adaptation to adverse environmental conditions is polyploidy with about twice as many species in temperate regions having two or more sets of chromosomes. Bliss (1962) considered that this was because: (1) there ~~are~~ is a high percentage of perennial herbs, (2) a relatively large number of grasses and sedges where polyploidy is high, (3) polyploids have wider tolerance limits. Elkington (1962) found that the number of chromosomes in plants of *Draba incana* from Upper Teesdale was similar to that recorded in more northern environments including South West Greenland and Iceland. The Flora Europaea indicates that this species is a robust biennial, although sometimes perennial. In Teesdale the plant is relatively long-lived but monocarpic. Thus it is clear that the environmental factors in Upper Teesdale affect the species in a very similar way to the climatic conditions in Arctic and Alpine regions of Europe, and indeed as we will see in the next chapter, climatic conditions in Upper Teesdale are similar to those of South West Greenland.

Grazing is an important factor in maintaining diversity in grasslands particularly the species rich grasslands of the chalk and limestone areas of Britain, which often support rare plants. In these situations a very delicate balance has to be achieved between the level of grazing required to maintain a sward in which the more sensitive herbs are able to survive, and that which causes destruction of the turf or alteration of species composition. The change in the composition of the vegetation brought about by changes in management have been studied on a number of occasions.

Exclusion of rabbits from a poor, acid grassland resulted, after 11 to 13 years, in the dominance of _Festuca ovina_ and the complete elimination of the accompanying species, Watt (1960). Study on the same plot was continued until 1969 giving 33 years of results which showed that from 1936 to 1954 the percentage cover of _Festuca ovina_ rose to a maximum of approximately 50%. This was followed by a fluctuating fall to a little over 20% in 1969. In the early stages following cessation of grazing the fescue flowered vigorously and no doubt the increase in this species was due to the successful establishment of seedlings. In the later stages as the plants became older they flowered less and the presence of increased litter provided an environment hostile to the establishment of seedlings, Watt (1971a).

Watt's study showed overall changes in floristic composition without reference to actual numbers of individuals. However, Williams (1970), using a pantograph, presented data on the survival of individuals of two species, growing in semi-arid desert grassland in Australia under grazed and ungrazed conditions. He found that under grazed conditions the sole representative of the original climax vegetation _Chloris acicularis_, had a very much reduced half-life value when compared with the plant under ungrazed conditions. Thus the absence of grazing tends to favour this species allowing larger and longer-lived crops. On the other hand _Danthonia caespitosa_, the disclimax dominant, which had a large population turnover was little affected by the presence or absence of grazing and there was a tendency for grazing to favour survival. *Chloris acicularis* was rapidly eliminated under grazed conditions and it would appear that this was due to an increased risk of mortality in the early stages of establishment.

An understanding of the stage in the life cycle of plants (particularly rare species) which is the most susceptible to changes in environmental conditions, is important in any management programme directed towards the conservation of the species concerned. Despite this there are very few studies which have attempted to record changes in the numbers of rare plant species under field conditions. The study of Tamm (1972a) on a number of orchid species, Watt (1971b) in the Breckland and Wells (1967) on *Spiranthes spiralis*, are of importance. Wells (1967) in particular illustrated the difficulty of identifying the many factors which together or separately may influence whether a plant flowers or remains in a vegetative state.

The overall effects of management on plant communities, especially those of significance for wildlife conservation, have received some attention. Harper (1971) reviewed some of the experiments including the Park Grass experiments at Rothamsted, which were started in 1856 to determine the effects of fertilizer treatments on the yield of a meadow grassland which had been in existence for several hundred years. There have been marked floristic changes in the plots which have now stabilised such that each plot has a unique species composition markedly different from the control.

Vegetational differences were observed between grazed and mown sections of a former hay meadow and the differences in species composition was attributed to the different treatments, Tamm (1956a).

The effects of sheep grazing as against mechanical cutting was considered by Wells (1971) in relation to the survival of chalk grassland communities.

The addition of fertilizer on a sward in Upper Teesdale dominated by *Kobresia simpliciuscula* was found to almost completely eliminate *Kobresia* from the turf and this was considered to be the result of stimulating the growth of competing grasses species by increasing the amount of available nutrients, Jeffrey (1971).

Other factors such as trampling and eutrophication, Streeter (1971) and walking and skiing, Bayfield (1971) have been considered in their effects on the species composition of chalk grassland at Box Hill and the vegetation of the Cairngorms respectively. At Box Hill species such as *Thymus drucei* and *Asperula cynanchia* were progressively eliminated from the turf subject to the highest visitor pressure. In the Cairngorms *Trichophorum cespitosum* and artificially sown S50 Timothy appeared to be less seriously affected by trampling than *Sphagnum*, lichens and *Calluna vulgaris*.

Interference between species and between individuals of the same species and the implications for the survival of plants in a certain vegetation type are discussed in Harper (1964) and Harper (1967). In the first of these papers Harper stresses the importance of the ability of a population to intercept the incident light with most plant species tending to develop until most of the light is trapped. In mixed stands the difference in growth habits of two species may determine the way in which the light resources are shared and lead to one species becoming dominant over the other. Perhaps eventually all the incident light may be trapped by the dominant species and this ability to put a canopy higher than that of the next plant may be an extremely important factor in bringing about vegetational succession.

Clearly this is not the full story since plant communities occur which have relatively stable mixtures of species, particularly so for climax communities. Experiments by Harper and McNaughton (1962) suggested that each species in a mixture of Papaver spp. was affected more by intraspecific competition than by interspecific competition (perhaps not surprising since each has similar growth form). For the species studied the risk of mortality of individuals increased with density. Thus there was an upper limit on the size of the population of each species regardless of sowing density. They argued that this intraspecific control is a necessary prerequisite if stable mixtures of species are to exist. If some control of this kind did not operate then the most aggressive species would become dominant to the exclusion of all other species.

The vegetation of any area results from a combination of many environmental factors acting in various ways, of which climate and soil are probably the most important, and affecting the ability of plant species to become established and maintain their populations. Over much of Britain the natural climax vegetation is deciduous woodland. However, there are very few areas of this vegetation type which are truly natural. Most of the 'natural' habitats including deciduous woodland have been affected to a greater or lesser extent by man and often the actual nature of the vegetation depends on the managemont regime imposed by man, as is the case with the chalk and limestone grassland of Great Britain.

Clearly the type of vegetation and its survival depends on the ability of the individual species to replenish their populations. In this context a knowledge of the life cycles of individual species and the stages which are most susceptible to mortality is important. This is particularly so where rare species are concerned as it may not always be enough simply to maintain the traditional management regime to ensure their continued existence. For example small changes in the intensity of grazing and fertilizer treatment may be enough to eliminate the more sensitive herbs from the vegetation.

In Upper Teesdale particularly in the grasslands associated with the outcrops of sugar limestone there are a large number of plants which are rare in the British Isles. An attempt has been made in this study to examine the way in which some of the plant populations behave under the present grazing regime. It is hoped that an understanding of the life strategies of some of the species will help to explain the long-term survival of the Teesdale 'rarities'. In particular a knowledge of the way in which individual species maintain their populations under the present management regime should aid their future conservation by allowing suitable long-term management of the vegetation to be recommended.

CHAPTER TWO

UPPER TEESDALE AND THE 'RARITIES'

Since 1843 when James Backhouse first published 'An Account of a visit to Teesdale in the Summer of 1843', and later wrote '. . . we set out for Widdybank Fell, Cauldron Snout and Falcon Clints; which comprehend a district probably the richest in Teesdale for botanists', (Backhouse Jun. 1844), botanists have been aware of its rich and varied flora. Baker and Tate (1868) listed 32 rarities from 'an area something like four square miles'. More recently Pigott (1956) listed about 140 rare or local plants from an area now almost wholly within the Upper Teesdale National Nature Reserve.

The flora of Upper Teesdale has been interpreted as a relict of a flora widespread in the late-glacial times, Godwin (1956). The existence of this and other refugia, largely depends on two environmental features affecting species survival through the post-glacial forest maximum; these were, no closed tree canopy and a relatively high calcium status of the soil, Pigott and Walters (1954). Pigott (1956) discusses a number of ecological factors which may have been important in maintaining the open conditions, particularly during the forest maximum. Some of these, including climate, geology and grazing, are discussed later. In addition to these, Clark, in Valentine (1965), suggests that moles may also have had some influence in maintaining open conditions, by breaking the vegetation cover and exposing the soil. He indicated that this may have been particularly important during the forest maximum when open habitats were at a premium and the survival of many of the Teesdale 'rarities' at greatest risk.

A detailed description of the history of the vegetation and flora of Widdybank Fell and the Cow Green reservoir basin in Upper Teesdale is given in Turner et al. (1973). The data presented indicates that even during the forest maximum the herb frequency in most of the pollen diagrams averaged 30% to 40%. This compares with a lowland diagram from Cranberry moss, Co. Durham, Turner (1970), where the herbaceous pollen grains represent only 5% of the total pollen. The conclusion drawn from these results was that the upland woods did not have a completely closed canopy like those of the lowlands and the relicts of the late-glacial flora survived in openings under the canopy.

Of 75 rare species of flowering plant described by Pigott (1956), 16 have pollen which can be identified to or very near the species level. Turner et al. (1973) reports that 11 of these 16 have been found in the post-glacial pollen record and concludes: 'The records of *Gentiana verna*, *Dryas octopetala*, *Betula nana*, *Saxifraga aizoides*, *Saxifraga stellaris*, *Helianthemum canum* and *Thalictrum alpinum* from zone O, the period of the forest maximum, confirm beyond any reasonable doubt that these rare species have indeed been in the area from the late-glacial to the present day. . . .'

Survival of so many rare plants in Upper Teesdale, particularly on Widdybank and Cronkley Fells, where the present study was carried out, was due to environmental factors allowing their survival through the forest maximum. Some of these, together with other factors including man, are still very important today.

The unique bedrock which outcrops on the two fells is undoubtedly one of the most important features of the area. Here the Melmerby Scar limestone has been recrystalised by the intrusion of molten magna, which cooled to form the Great Whin Sill, to a saccharoidal marble. Where the metamorphosed limestone outcrops and is not covered by glacial drift, freely draining, unstable soils have developed. Formation of the calcite sand, the 'sugar limestone', is largely the result of sub-surface weathering of the marble beneath the layer of drift or soil, Johnson et al. (1971). Johnson suggests that sub-surface weathering followed by erosion of the unstable calcite sand, have provided a succession of open habitats in which the rare plants have survived.

The key to the ecological factors important to the survival of the rare plants, after clearance of the forest, would appear to be the reduction of the competitive ability of some of the more vigorous species invading the area. Climate is perhaps one of the factors which in the past restricted the growth of trees and today may be important in restricting the growth of competitors.

Manley (1936) considered the climate at Moor House (now within the National Nature Reserve) at 561 metres above sea level (the Widdybank Fell station is at 500 metres), to be at the upper limit of cultivation in England. He describes a bleak climate, which is windy and damp where climatic data correspond well with records at sea level in Southern Iceland. Comparison of the yearly figures for the mean air temperature and rainfall for the two stations, at Moor House and

Widdybank Fell (see Table a) indicates that the climate was slightly more extreme at Moor House.

The air temperature was slightly higher on Widdybank Fell than at Moor House. There was very little variation between years except in 1971 when the temperature was much higher at both stations than in the other years. The rainfall at Moor House was higher in all years than that recorded on Widdybank Fell. The difference varied from nearly 152 millimetres in 1968 to only 18 millimetres in 1969. Although the variation between years was quite large, the most unusual year was 1971 when the rainfall was exceptionally low.

Data are presented in Figure 1 and show the monthly figures for mean daily air temperature $\frac{1}{2}$(max. + min.) and monthly rainfall over the period of study on Widdybank Fell. In 1970 following a late Spring the temperature rose sharply in May and June. During these months not only were the mean temperatures higher than in the same months in any of the other years, but also they were the driest. The mean temperatures in 1970 remained high until September and it would appear that the climate was particularly favourable to plant growth and development. Data are presented in the chapters on the individual species which show that vegetative reproduction for some of the species was noticeably higher in that year than in the other three.

Another factor, <u>low availability of phosphate</u>, was found by Jeffrey (1971) to be important in reducing the competition of two potentially fast-growing grass species, in a <u>Kobresia</u>-rich sward. He also considered climate, grazing and trampling and heavy metal toxicity to be other likely factors of importance.

Table a

SUMMARY OF MEAN DAILY AIR TEMPERATURES $\frac{1}{2}$(MAX. + MIN.) AND RAINFALL ON WIDDYBANK FELL AND AT MOOR HOUSE

	1968	1969	1970	1971	1972
Mean daily air temperature, °C.					
Widdybank Fell	5.4	5.4	5.5	6.4	5.5
Moor House	4.9	4.7	4.9	5.6	4.8
Rainfall in millimetres					
Widdybank Fell	1,572	1,654	1,849	1,295	1,671
Moor House	1,976	1,671	2,141	1,346	1,788

Bellamy et al. (1969) found that communities containing arctic alpine species (the relicts from the late-glacial flora) had an annual dry weight shoot production of less than 150 glm^2. They went on to compare figures for shoot production for a range of true alpine tundra ecosystems given by Bliss (1966), with those obtained in Teesdale. They concluded that, 'Teesdale ecosystems seem to have much in common with true ~~alpine~~ arctic tundra ecosystems'. Thus, it would appear that the Teesdale 'rarities' survive in communities which correspond closely to ~~alpine~~ arctic communities and that this is probably due to the cold and wet climate and low nutrient availability.

Grazing is a factor which today plays an extremely important part in the maintenance of these open ecosystems. It is clear from the appearance of grassland which has been fenced that the absence of grazing leads to a much more vigorous growth of the vegetation. It seems probable that in time, some of the species less tolerant of competition would be eliminated from the sward if grazing were prevented entirely. Casual observation inside the Meteorological Station enclosure indicates that *Gentiana verna* is able to survive in the ungrazed closed *Sesleria caerulea* turf but *Gentiana verna* plants, in turf transplanted from below top water line to the University of Durham, were lost from the turf within 18 months. During this period, *Sesleria caerulea* grew quite vigorously as did several of the other species in the sward, including *Primula farinosa*. The effects of grazing animals may also have been important in helping to prevent complete closure of the tree canopy by trampling and prevention of regeneration, particularly around springs.

Clearly a variety of factors have been important in the long term survival of plant communities in which the rare species occur. However, throughout this period up to the present day survival of individual species will have depended entirely on their ability to produce new individuals to make up the losses brought about by mortality. This ability would also need to be flexible enough to overcome different environmental conditions, ranging from very cold open tundra, through open forest to the present day where the vegetation of the 'sugar limestone' turf is held at an artificial stage of succession by grazing.

Grazing, as has already been indicated, is important in reducing the competition from species likely to eliminate some, if not all, of the Teesdale 'rarities'. Grazing by sheep on Widdybank Fell, and sheep and rabbits on Cronkley Fell also has an effect on some of the rare plants themselves by restricting their ability to reproduce sexually. As will be seen later, (in Chapters four to nine), this is of considerable importance for some species where almost all the flowers are removed by grazing, before they are able to produce seed. This means that some species must be able to reproduce vegetatively at a rate which will allow for the replacement of the population.

The species chosen for study were selected from 18 for which quadrats were initially established. The 6 dealt with in detail show a variety of life strategies.

These species are included in a number of different geographical elements which come together in Upper Teesdale. A detailed description of the geographical elements of the 'Teesdale assemblage' of plants is given by Bradshaw (1970). Most of the species have an arctic-alpine or northern distribution although *Helianthemum canum* and *Hippocrepis comosa*, which both occur only on Cronkley Fell, are continental southern species, and in their most northern and highest station in Britain.

The geographical elements of the species included in this study, Bradshaw (1970), are as follows:-

Carex ericetorum *Polygala amarella* *Viola rupestris*	Continental Northern
Draba incana	Arctic-alpine
Gentiana verna	Alpine

Linum catharticum and *Viola riviniana* are much more widely distributed and *Viola rupestris x riviniana* is not known from any other station in Western Europe.

Distribution of some of the individual species in Britain is very restricted. In the case of the hybrid violet, as far as can be ascertained, Widdybank Fell is the only station in Britain or Europe. *Carex ericetorum* is rather more widespread, occurring on calcareous soils from Suffolk to Westmorland (Clapham, Tutin and Warburg). *Polygala amarella* is restricted to a very few areas in Western Yorkshire and Durham. *Viola rupestris* occurs at only three sites in Britain, all in the North of England, where the populations are fairly small. *Draba incana* is rather more widespread occurring from sea-level to up to 3,550 feet on Ben Lawers and northwards from Caenarvon, Stafford and Derby to Orkney and Shetland (Clapham, Tutin and Warburg, 1962). *Gentiana verna* occurs in only two areas, Upper Teesdale and the Burren in Western Ireland, and in both areas the species is quite widespread although by no means common. *Linum catharticum* and *Viola riviniana* occur commonly throughout Britain.

The communities in which these species, and many of the other Teesdale 'rarities', occur are described in Pigott (1956). More recently Shimwell (1969) described the status of the Class Elyno-Sesleriatea Br.-Bl. 1948 in the British Isles. This Class comprises most of the calcareous grass-heaths of the arctic-alpine regions and in Britain, communities in which *Sesleria caerulea* is dominant or co-dominant occur in a marked zone across Northern England, forming a phyto-geographical link between the Classes *Festuco-Brometea* (lowland grasslands) and *Elyno-Seslerietea*. These grasslands are referable to the Sub-alliance *Seslererio-Mesobromion* Oberd. 1957 of the Class *Festuco-Brometea* Br.-Bl. and R.Tx. 1943. A detailed study has been carried out by A. V. Jones (1973) of the phytosociological groups on Widdybank Fell. Vegetation maps of the whole Fell have been produced at a scale of 1:10,000 and of those areas of particular phytogeographic interest, including the areas of 'sugar limestone' grassland at a scale of 1:2,500.

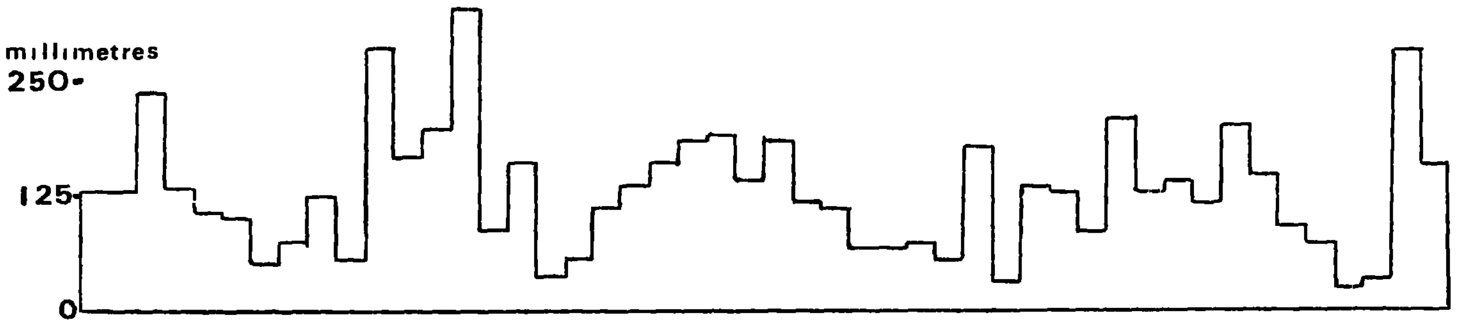
Figure 1

WIDDYBANK FELL

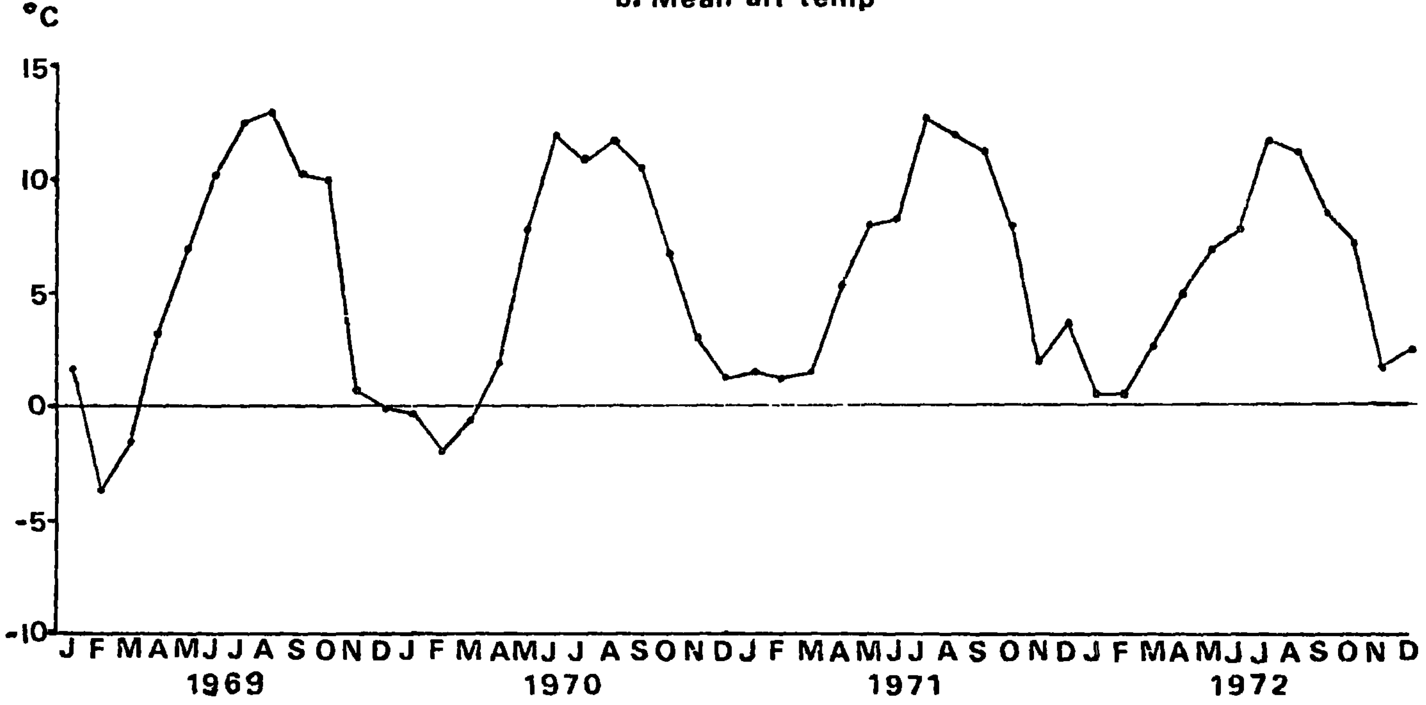
(a) Rainfall (millimetres)

(b) Mean Air Temperature °C.

FIGURE 1. Widdybank Fell a.Rainfall



b. Mean air temp



CHAPTER THREE

METHODS

SECTION 1: SELECTION OF SAMPLE AREAS

In July 1968 work was started by a Research Assistant, Miss Maureen E. Watson, into the selection of the best sites, each containing several species and where possible a reasonable number of plants. Initially, a total of 18 species were chosen for study, but some of these were discounted together with their quadrats, in order that a more intensive study could be made on a smaller number of species. In this context, additional quadrats were established after 1968 so that some species of plants could be studied in different situations and greater numbers of individuals could be identified. (Records were kept on other species which were not studied as intensively and not included in the main body of the thesis).

The sites were situated on closely grazed sugar limestone turf and in areas of eroding sugar limestone mostly on Widdybank Fell but also on Cronkley Fell. Initially, these were chosen so that records could be kept for each species at three different distances from the eventual top water level of the reservoir; within 100 metres, approximately 200 to 250 metres and over 500 metres. In fact, over the study period reported here there is no indication from the results of differences in the performance of the species at the varying distances from the reservoir. Reference to this, therefore, has been ignored, although the study of these species, which is being continued, may provide some information if there are any long term effects brought about by the close proximity of a large water body.

The selection of the 'best' areas for establishing quadrats and sample sites was facilitated by maps showing the detailed distribution of a number of characteristic species of the Teesdale flora, produced by voluntary workers under the guidance of Dr. M. E. Bradshaw. Due to the very restricted nature of some of the populations in Teesdale, the number of possible areas which could have been sampled varied a great deal between species. Details of the sites, their permanent quadrats and sample sites, are given in Section 3.

Sites 1, 2 and 3 in Section 3, Table a, were situated close to the top water-line of the reservoir. Site 1, which contained only one permanent quadrat and sample site, was situated in sugar limestone turf near to Slapestone Syke. Site 2 was also on sugar limestone turf, in this case periodically disturbed by moles. Three years after the study ended, this area was covered by the wind blown sugar limestone sand. This sand was formed by the erosion of the sugar limestone turf, exposing the underlying soil and rock by wave action, where the outcropping metamorphosed limestone forms the reservoir shore. Site 3 was situated on closed heavily grazed sugar limestone turf.

Sites 4, 5, 6 and 7 were situated at approximately 200 to 250 metres from the top water-line of the reservoir. Site 4, a small area of apparently heavily grazed sugar limestone turf, was close to a spring often frequented by sheep. Site 5 had a single long quadrat running along a very open eroding edge of sugar limestone, where the vegetation cover was very sparse. Sites 6 and 7 were situated on closed sugar limestone turf with Kobresia simpliciuscula. One of the quadrats and its associated sample site also had Calluna vulgaris.

Sites 8, 8B and 9 were more than 500 metres from top water-line of the reservoir. Sites 8 and 9 contained both closed and eroding limestone turf, the former with Calluna vulgaris in one quadrat. Site 8B was situated on grazed limestone turf with Calluna vulgaris and Empetrum nigrum present.

Site 10 was also situated on sugar limestone turf on Cronkley Fell, with one quadrat inside a rabbit and sheep-proof exclosure. The other quadrat and associated sample site area were heavily grazed by rabbits and sheep and contained Calluna vulgaris and Empetrum nigrum.

SECTION 2: THE INDIVIDUALS STUDIED

The study of plant population dynamics has been hindered by problems relating to the definition of 'the individual'. Harper (1967), considered that this was due to the effect of two interlinked properties of higher plants - plasticity and vegetative reproduction. More recently, Sarukhan and Harper (1973), stated that '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'. Plasticity can to some extent be measured by counting the number of seeds produced by a reproductive unit, but the definition of that 'unit' remains a problem.

The successful establishment of a single seedling may result in the production of large numbers of offspring identical to the original parent and which may or may not remain a part of the parent. Clearly, in this situation an arbitrary decision has to be made if the plant population is to be subject to numerical analysis, Harper (1967).

Observations on the clone size of *Festuca rubra*, *Festuca ovina* and *Trifolium repens*, Harberd (1961), (1962) and (1963) respectively, indicated that the age of the clones must be measured in hundreds of years. Under these circumstances in plant populations, there are two levels of population behaviour, Harper and White (1974); the number of colonies (clones derived from one seedling) and the number of members of that colony (shoots). Where plant species do not reproduce vegetatively, the second level of population organisation may be considered to be related to the birth and death of parts of a plant (such as a leaf or root).

It is applicable in this study to consider the two levels of population behaviour as they relate to the production of a new plant from seed (genet), or by vegetative reproduction resulting in discrete functional units (ramets), Kay and Harper (1974). Clearly, where an individual appears as a result of seed germination and the establishment of the seedling, the unit is easily defined. However, if this unit produces shoots or lateral branches, care must be taken in deciding which is the *functional* unit to be considered.

Of the 18 species which were originally chosen for the study, 6 were recorded in detail and the results are given in Chapters four to nine inclusive. Data from another 2 species are included in Chapter ten. The 8 species represent a variety of life strategies and in each case the 'unit' has been described in the appropriate chapter. One of the criteria for its definition is that it should be an identifiable entity capable of reproduction. The term 'unit of reproduction' has been used to describe the individuals in the populations.

Three of the species reproduce entirely by seed production and the establishment of seedlings. Linum catharticum is a biennial and both the first and second year plants are easily identifiable. Draba incana is a mono-carpic perennial and Polygala amarella a poly-carpic perennial. In each of these 3 species a 'unit of reproduction' is equivalent to the 'genet' of Kay and Harper (1974) and is any plant which arises from one seed. In each case, although the mature plant on flowering produces branches, they are clearly attached to the main stem of the original plant, which developed from a seedling.

Viola rupestris and Viola riviniana are perennials which reproduce both by means of the production of seed and vegetative shoots. In these species plants which develop from seed are clearly 'units of reproduction' forming a rosette of leaves from which flowering branches (attached to the main stem) are produced. These plants (genets) also produce vegetative shoots (ramets) which in the former species are less easy to define.

New vegetative rosettes are sometimes produced by Viola rupestris on the underground stem. Although these do not seem to develop a separate root system they are, in appearance, discrete plants and able to produce flowers and set seed. Usually, it was not possible to determine the connections between the mother plant and these rosettes and, therefore, they have also been considered as individuals for the purpose of this study.

In _Viola riviniana_, the new vegetative rosettes arise from root shoots and become established as independent plants which are able to flower and set seed. These individuals are equivalent to the 'ramet' of Kay and Harper (1974). Once the vegetative shoots of both _Viola rupestris_ and _Viola riviniana_ become established, it is impossible, in both species, to distinguish between plants which have developed from seed or vegetative shoots. Because of this each rosette has been treated as being of equal importance.

Gentiana verna and _Carex ericetorum_ reproduce by means of the production of vegetative shoots. Both species are able to produce seed although no seedlings were recorded during the study period. All of the units in these species are equivalent to the 'ramets' of Kay and Harper (1974) and both have distinct rosettes which are able to produce flowers and ripe fruits. The connections between the rosettes are impossible to determine without uprooting the plants and these are considered, therefore, to be the 'units of reproduction'. _Viola rupestris x riviniana_ is exceptional in that the rosettes are not capable of producing seed, as the flowers are sterile. However, each of the shoots are similar to those of _Viola rupestris_ and are, therefore, also considered to be the 'units of reproduction' (the individuals of this study).

SECTION 3: PERMANENT QUADRATS AND SAMPLE SITES

Once the sites had been selected for study, permanent quadrats and sample sites were established. At each site the permanent quadrats were chosen so that detailed monitoring of the individual plants of the species being studied could be carried out.

All the permanent quadrats were 30 centimetres wide, but varied in length from 0.5 to 5 metres, depending on the density of the species being studied. These quadrats were permanently marked with plastic coated, metal corner pegs sunk to ground level, the pegs being located by use of a compass bearing and known distance from an easily-found landmark. Since the main purpose of this study was to monitor the behaviour of plant populations under natural conditions, it was important that any system for marking the quadrats should have a minimum influence on the vegetation and be inconspicuous so that it did not attract visitors.

Larger permanently-marked sample sites were required to supplement the size of the sample of flowering and fruiting plants and their seed production. Where possible these were situated close to a permanent quadrat and in a similar vegetation type. A complete list of permanent quadrats and sample sites is given in Table a, together with the species studied in each, and the quadrat size. More detailed descriptions of vegetation in the permanent quadrats are given in Chapters four to nine, Section 2, where 6 of the species, *Viola rupestris*, *Viola riviniana*, *Viola rupestris x riviniana*, *Polygala amarella*, *Draba incana* and *Gentiana verna* are described in detail. Information on the other species studied in less detail, *Linum catharticum* and *Carex ericetorum* are included in Chapter ten.

The vegetation in some of the permanent quadrats was mapped and where plans of these are available they are included under the appropriate species heading. A symbol represents the species which covers more than 50% of each centimetre square; where 2 species cover a square equally, both symbols are given; where several species contribute to the cover the square is represented by a cross.

Table a

PERMANENT QUADRATS AND SAMPLE SITES

SITE	Permanent Quadrat No.	Sample Site No.	Size in Metres	Species Studied
1	1.1		0.3 x 2.5	Gentiana verna
		1ss1	0.8 x 3.0	Gentiana verna
2	2.1		0.3 x 2.5	Linum catharticum Draba incana
		2ss1	2.0 x 4.5	Linum catharticum Draba incana
	2.2		0.3 x 4.0	Viola rupestris
		2ss2	2.0 x 6.0	Viola rupestris
	2.3		0.3 x 1.0	Viola rupestris
3	3.1		0.3 x 3.0	Viola riviniana
	3.2		0.3 x 2.0	Viola rupestris
	3.3		0.3 x 1.0	Viola rupestris x riviniana
	3.4		0.3 x 2.0	Viola rupestris
	3.5		0.3 x 1.0	Viola riviniana
		3ss1	1.2 x 2.0	Viola rupestris
		3ss2	0.7 x 1.7	Viola rupestris x riviniana
		3ss3	0.3 x 1.0	Viola riviniana
4	4.1		0.3 x 3.0	Gentiana verna
		4ss1	1.5 x 1.5	Gentiana verna
5	5.1		0.3 x 5.0	Draba incana Linum catharticum

SITE	Permanent Quadrat No.	Sample Site No.	Size in Metres	Species Studied
6	6.1		0.3 x 4.0	Polygala amarella Viola riviniana
	6.2		0.3 x 5.0	Viola rupestris
		6ss1	1.0 x 1.0	Viola riviniana
		6ss2	4.0 x 5.0	Viola rupestris
7	7.1		0.3 x 2.0	Polygala amarella
	7.2		0.3 x 3.0	Polygala amarella Gentiana verna
		7ss1	3.0 x 3.5	Gentiana verna Polygala amarella
		7ss2	1.5 x 3.0	Polygala amarella
	7.3		0.3 x 2.0	Draba incana Polygala amarella
8	8.1		0.3 x 2.5	Draba incana Carex ericetorum
		8ss1	1.0 x 2.5	Draba incana
	8.2		0.3 x 2.0	Carex ericetorum
	8.3		0.3 x 1.5	Gentiana verna
		8ss3	2.0 x 2.2	Gentiana verna
8B	8B.1		0.3 x 1.0	Gentiana verna
		8Bss1	1.0 x 2.0	Gentiana verna
	8B.2		0.3 x 2.0	Viola riviniana
		8Bss2	0.7 x 1.2	Viola riviniana
9	9.1		0.3 x 0.5	Viola rupestris x riviniana
		9ss1	0.5 x 0.8	Viola rupestris x riviniana

SITE	Permanent Quadrat No.	Sample Site No.	Size in Metres	Species Studied
9	9.2		0.3 x 2.0	Viola rupestris
		9ss2	1.0 x 1.5	Viola rupestris
	9.3		0.3 x 1.0	Viola rupestris
		9ss3	1.0 x 2.5	Viola rupestris
10	10.1		0.3 x 2.0	Gentiana verna
	10.2		0.3 x 3.0	Polygala amarella
		10ss2	1.0 x 3.0	Polygala amarella

SECTION 4: METHOD OF RECORDING

Once the permanent quadrat had been located on the ground, a metal frame 30 centimetres by 100 centimetres with a movable cross-piece, both marked in half centimetres, was placed over this marked area. By placing the frame in exactly the same place on successive visits, individual plants could be identified and their fate recorded. This is similar to the method used by Watt (1960) and Tamm (1948, 1956a and 1972a and b).

Detailed monitoring of individual plants, including very small seedlings, at about 1,600 feet above sea level, in an area characterised by 60 to 70 inches of rain per year and almost constantly windy conditions presented some problem in recording. However, the method adopted, which is described below, allowed for accurate recording of all the individuals within each permanent quadrat.

Each plant (of the species being recorded) was originally identified by the co-ordinates of the frame. These were plotted on graph paper (scale 10:1) which was then placed in a thin plastic bag and sealed with P.V.C. adhesive tape, (the tape and adhesive is waterproof). A semi-matt overlay ('Permatrace' drafting film) was attached to the plastic bag with the matt surface uppermost, and the corners of each metre were marked on this overlay. Records of the plants at each visit were marked on the overlay using Staedtler-Mars 'lumochrom' leads which are waterproof. Sagar (1959) describes the use of a pantograph for recording Plantago lanceolata, but for much smaller plants on the uneven ground and in the windy and wet conditions this method would not have been suitable.

All plants, which were present at the end of a growing season, were marked on a new chart. Reference was made to these charts throughout the following year when the fate of the individual, that is whether it flowered, when it died, etc., was recorded on the overlay. All additions, both seedlings and new vegetative shoots, were also recorded. A different coloured lead was used for each visit and the date and all the changes were recorded in the colour of the visit. In this way, within any one permanent quadrat, the number of individuals, their fate and reproduction, (in terms of new vegetative shoots or seedlings), was followed.

At the end of each growing season the charts, together with their overlay, were carefully checked. Individual plants were identified by their co-ordinates in each metre length of the permanent quadrats, and in this way not only was the fate of new individuals recorded, but also that of plants surviving from previous years.

The larger permanently-marked sample sites were recorded each year, when the total number of individuals was counted and the number of these which flowered noted. At each site attempts were made to count the number of buds, flowers and fruits per flowering plant and the number of seeds per capsule from a sample of 30 flowering plants and 30 capsules (one from each of 30 plants). In some areas, for some species, a sample of this size could not be collected and data for the number of seeds per capsule were often only obtained by collecting from the whole of the Fell. Removal of the inflorescences by grazing also prevented complete records from being obtained for the number of flowers and fruits produced for some species.

SECTION 5: DATA PRESENTATION

The total number of individuals in each permanent quadrat, the *total population* or *quadrat population*, includes *all* the surviving individuals, *all* new vegetative shoots as they appear and seedlings which have survived to their second year. These records were made at least three times in any one year, although, in 1969, due to changes in personnel, some of the mid-season records were not made. Three main periods of recording were recognised in the months of May and June (Spring), July and August (Summer) and September and October (Autumn). These data are plotted on 2 or 3 cycle log-normal graph with the date of recording visible along the horizontal axis. For each of the 6 species reported in Chapters four to nine the total populations are shown separately for each permanent quadrat.

The number of individuals recorded in each quadrat when it was first established, (*the original quadrat population*), consists of individual plants of varying ages. The survival of these mixed-age populations are shown by survivorship curves plotted on log-normal graph paper for each species. Half-life values, based on the decay of these groups of individuals from the time the quadrat was established to Autumn 1972, have been worked out using the formula characterising the decay of a radioisotope:

$$\lambda = \log \frac{No}{Nt} / t$$

$$\text{Half-life } \tau = \log_e 2 / \lambda$$

λ is a constant; No the total number of individuals initially recorded in each quadrat; Nt is the number of these surviving after time t.

This formula assumes that the risk of mortality is independent of the age of the individual. This is true for almost all age groups of plants except seedlings of Draba incana, where the risk of mortality is much increased in the early stages of seedling establishment. Plants appearing first as seedlings have not been included in the total populations or the original populations until their second year. Thus, since the mortality curves of all other age-groups of individuals are linear, indicating a constant risk of mortality, it is considered that the above formula can be used.

Seasonal survival over six-monthly periods (corresponding roughly to the Summer and Winter months) have been given together with the standard error. The rate of survival (q) is expressed as the proportion of the individuals at risk (No) which survive to the end of the time period (Nt).

Thus $q = Nt/No$

Standard error $= \sqrt{p \times q/N}$

Where p is the rate of mortality
q is the rate of survival
N is the total number of individuals 'at risk'

Seedlings less than one year old are not included in the number of plants considered to be 'at risk', in an attempt to exclude any disproportionate effects which might result from increased mortality of seedlings during the initial stages of establishment.

Recruitment of both new vegetative shoots and seedlings appearing in each of the permanent quadrats is expressed as an annual rate per individual present in the total population. In some cases recruitment is a continuous process with seedlings and vegetative shoots appearing throughout the growing season. Here recruitment is expressed as a rate per individual present at the time of the Summer recording. In some species, recruitment of seedlings occurs over a relatively short period; this is particularly so for *Draba incana*, *Viola rupestris* and *Viola riviniana* where germination takes place in the Spring. In these species annual seedling recruitment is expressed as a rate per individual present in the Spring of each year.

Survival of groups of individuals of known age is shown graphically, plotted on log-normal paper. For each species, all individuals 'born' at the same time within each of the permanent quadrats are summed for each year. Seedlings and vegetative shoots are treated separately, the term 'born' indicating the appearance of a new vegetative shoot or seedling between successive visits.

The behaviour of the individuals in each quadrat is shown by diagrams similar to those of Tamm (1948, 1956a and 1972a,b); some reproduced in Harper (1967). Individual plants are represented by a single vertical line taken in sequence from one end of the permanent quadrat to the other. Time is represented on the vertical axis and lines starting at the base represent individuals in the initially recorded, mixed-age population. Lines starting further up the time scale represent additional individuals, both vegetative shoots and seedlings. Where vegetative reproduction has been observed additions are shown as continuous lines (see *Gentiana verna*). Additional seedlings are represented by a broken line for their first year only, and thereafter by a continuous line. (Note that in the case of *Draba incana* many seedlings appear in the Spring and have a high rate of mortality during their first few months. Surviving individuals are not, therefore, included in the diagram until the Autumn).

Reproductive performance for species where seed is produced under grazed conditions, *Viola rupestris*, *Viola riviniana*, *Polygala amarella* and *Draba incana*, is expressed as the number of seeds produced per 100 plants in both permanent quadrats and sample sites. Where applicable, this figure is given for the values summed between sites and between years. These figures give an indication of the actual number of potential new individuals (seeds) which are produced. Where possible these figures are based entirely on the data collected at each site. However, as already indicated, complete data are not always available and for some of the species overall values for some parameters (particularly seeds/capsule) have been used in estimating seed production.

CHAPTER FOUR

VIOLA RUPESTRIS

SECTION 1: INTRODUCTION

Viola rupestris is a small rosulate plant, with a short, central shoot, a basal rosette of leaves and axillary flowering stems (Flora Europaea). Lateral branches, often underground, give rise to rosettes and so form a type of vegetative reproduction. As far as can be ascertained these branches do not develop a separate root system and should not be regarded as true vegetative reproduction. However, it is usually impossible to determine the connections without disturbing and destroying the plant, therefore, the individual or 'unit of reproduction' has been defined as any rosette which arises from a seed or underground stem.

Individual plants are perennial and relatively long-lived dying down during the winter period, although in Teesdale sometimes one or two small leaves are visible which often develop a purple colouration. Some exposed stems of plants growing on bare eroding sugar limestone, show scars of previous years' leaves below the current year's leafy rosette. The number of scars indicate that a few plants may be quite old and the quadrat populations have a high proportion of mature individuals.

In open habitats flowering is **prolific**. This is in sharp contrast to the areas where plants are growing in closed turf and only limited numbers of flowers are produced. Flowers are of two kinds; chasogamous (open) and cleistogamous (closed). The latter inbreeding mechanism produces most seed;

open flowers are usually lost before ripe seed can be produced as their peduncles are long enough to raise the flowers above the leaves, making them more conspicuous and resulting, perhaps, in their being eaten by sheep.

Replacement of the population is slow and dependent both on vegetative and sexual reproduction. The relative importance of these two modes of reproduction depends to some extent on the habitats in which the plants are growing. Establishment of seedlings is more important in the open habitats where relatively large numbers of ripe seeds are set. In the closed sward where individuals are widely spaced, a small number of flowers produce much smaller numbers of seed than in the more open areas and seedlings are relatively few. The very open site at 9 was an exception to this general rule in that although flowering and seed-set was quite prolific only one seedling had been recorded in the permanent quadrat during the study period.

SECTION 2: PERMANENT QUADRATS

Four sites were selected on the sugar limestone soils of Widdybank Fell for the study of Viola rupestris. They fall conveniently into two broad types; one where the vegetation was open, flowering relatively prolific and the plants closely grouped, the other where the vegetation was closed, flowers few and the individuals widely spaced. The open communities occurred at site 2 near the reservoir's edge and site 9 which was furthest from the reservoir on Widdybank Fell. Quadrats selected in closed communities were situated at sites 3 and 6, the former on a south west facing slope just above the reservoir, the latter some 200 metres further away.

Details of the vegetation in each of the seven permanent quadrats are given below. Sample metres have been mapped for quadrat 3.4 which had an almost completely closed turf and quadrat 9.3 which had a very open vegetation and was situated on eroding sugar limestone (Figures 2 and 3).

Quadrat 2.2 (disturbed) had a vegetation cover which was relatively open being periodically disturbed by moles. Festuca ovina was the dominant species with Sesleria caerulea, Minuarta verna, Koeleria gracilis, Thymus drucei, Helianthemum chamaecistus, Briza media and Carex flacca also present.

Quadrat 2.3 (± open) was situated in an area of open eroding sugar limestone a few yards from 2.2, which had approximately 13% of the quadrat without vegetation cover. Sesleria caerulea and Festuca ovina were dominant, with Thymus drucei, Helianthemum chamaecistus, Koeleria gracilis, Draba incana and Minuartia verna among the other species present.

Quadrat 3.2 (closed) had an almost complete cover dominated by Festuca ovina and Sesleria caerulea with Kobresia simpliciuscula quite common in the sward. Other species present included: Helianthemum chamaecistus, Antennaria dioica, Plantago maritima, Lotus corniculatus, Carex capillaris, Selaginella selaginoides, Gentiana verna, Potentilla erecta, Gentianella amarella and Thymus drucei.

Quadrat 3.4 (± closed) had a vegetation similar to that for quadrat 3.2 although a little more open and a plan of a sample one metre in length is shown in Figure 2. The turf was dominated by Sesleria caerulea and Festuca ovina with Plantago maritima, Hieracium pilosella, Kobresia simpliciuscula, Thymus drucei, Helianthemum chamaecistus and Selaginella *selaginoides*. It can be seen that the vegetation was relatively open with a few *Viola rupestris* plants which were widely spaced.

Quadrat 6.2 (closed) was situated in another area where the sward was almost completely closed with *Sesleria caerulea* and *Festuca ovina* dominant. As in quadrats 3.2 and 3.4 plants of *Viola rupestris* were widely spaced and few in number. *Kobresia simpliciuscula* was also present in the quadrat togethor with *Polygonum viviparum*, *Linum catharticum*, *Primula farinosa*, *Thymus drucei*, *Briza media* and *Helianthemum chamaecistus*.

Quadrats 9.2 (± open) and 9.3 (open) were both relatively open and situated on very dry eroding sugar limestone. Plants of *Viola rupestris* were present in relatively large numbers, grouped closely together. *Sesleria caerulea* and *Festuca ovina* were dominant with *Thymus drucei* and *Helianthemum chamaecistus* among the other species present. Quadrat 9.3, the vegetation of which is shown in Figure 3, was very open with 45% of the area bare ground or covered by a low cushion of moss/lichen with *Tortella tortuosa* the dominant moss. Quadrat 9.2 had a much more dense vegetation with only 17% of the area bare ground or covered with moss/lichen. In this quadrat the vegetation was rather taller than that in quadrat 9.3 although not as dense as the quadrats at sites 3 and 6.

One sample site for the recording of reproductive performance was situated at each of the sites 2 and 3 and quadrats 6.2, 9.2 and 9.3 each had a sample site associated with them. Details are given in Chapter three.

Figure 2

MAP OF VEGETATION IN QUADRAT 9.3

Viola rupestris

FIGURE 2. Map of Vegetation in quadrat 9·3 - Viola rupestris (July 1970).

KEY to main species : • Sesleria caerulea, / Festuca ovina, A. Minuartia verna, T. Thymus drucei, O. Viola rupestris, α. moss, β. Lichen, To. Tortella tortuosa.

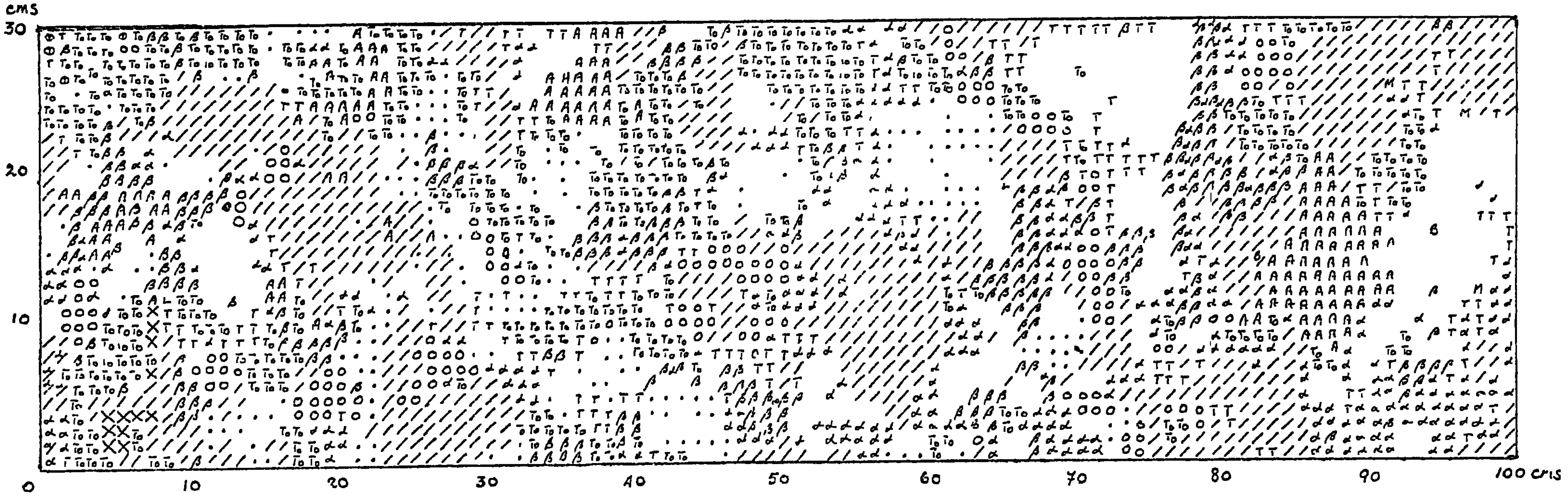


Figure 3

MAP OF VEGETATION IN QUADRAT 3.4

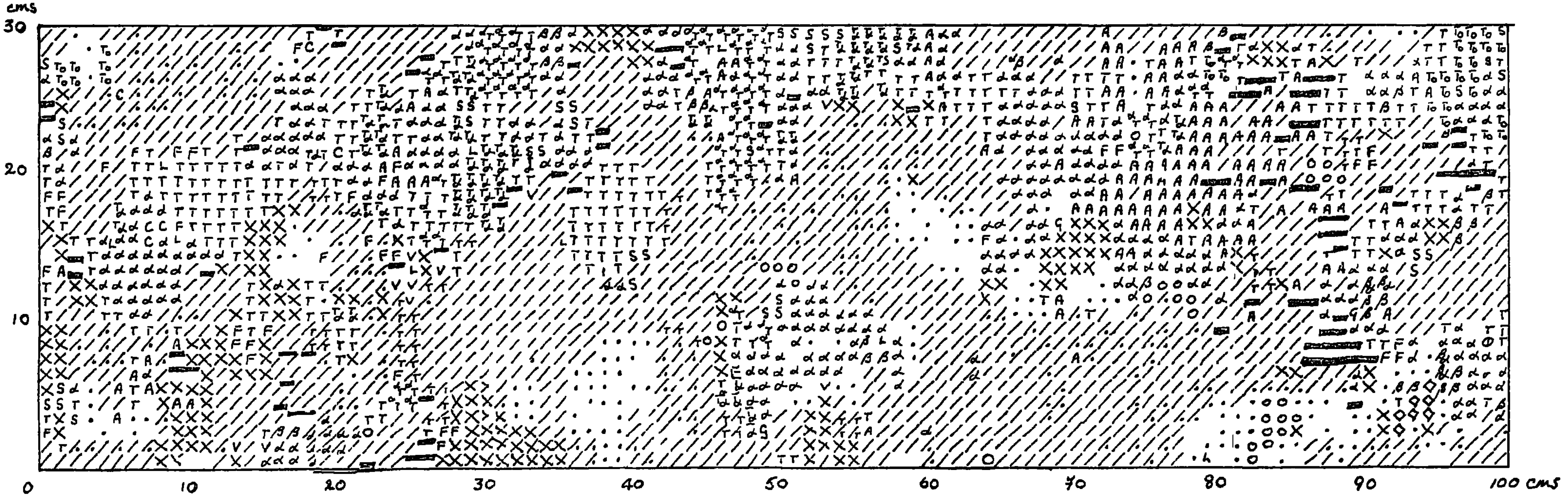
Viola rupestris

FIGURE 3. Map of Vegetation in quadrat 3·4 - Viola rupestris (July 1970).

KEY to main species: • Sesleria caerulea, / Festuca ovina, ▬ Kobresia simpliciuscula,

A Helianthemum chamaecistus, O Viola rupestris, T Thymus drucei

α moss cover.



SECTION 3: POPULATION FLUX

Over the period of recording, the total number of individuals in each quadrat remained at or above that of the originally recorded mixed-age population (Figure 4). Increases in the number of individuals ranged from 55% for quadrat 2.3 to 10% for quadrat 3.4. Only quadrat 9.3 did not show any overall increase, in fact an increase in 1972 was preceded by a decrease in 1971 such that the quadrat population in the Autumn of 1972 was the same size as the original population.

Change in the quadrat populations from season to season was irregular with increases in the number of individuals occurring both during the Summer months and between the Autumn and Spring records. Where there was an overall loss of individuals from the quadrats, this usually occurred during the Summer months.

Survivorship curves for the originally recorded mixed-age population in each quadrat are shown in Figure 5. The curves are remarkably linear indicating that over the period of recording the rate of loss of individuals remained constant, i.e. the risk of mortality was independent of their age. Only quadrat 6.2 showed any sudden decline in numbers and this was due to the loss of a group of individuals in 1969, which may have been uprooted by sheep. Superimposed on these curves there is a seasonal oscillation which indicates that there was a greater risk of mortality during the growing season. This is particularly marked in the curve for the original population in quadrat 9.3 where in both 1970 and 1971 the gradient dips quite steeply over the summer months.

Linear survivorship curves showing similar seasonal oscillations were also obtained for Plantago lanceolata, Sagar (1959) and mature populations of three species of buttercup Sarukhan (1971). In the first of these studies the slope of the curves was steeper between April and June and in the second during Spring and early Summer. Sarukhan and Harper (1973) suggest that the demands for limited resources may be responsible for regulating mortality in the three species of buttercup and that rigours of climate play only a minor role, a conclusion which might seem also to apply to Viola rupestris.

The survivorship curves for Viola rupestris are relatively shallow in addition to being linear, indicating that the rate of turnover of individuals is slow. Half-life values based on the decay in the number of individuals in the original population over the period of recording (see Table a) indicate that the time taken for complete replacement of individuals may take as long as 32 years.

The half-life values show a two-fold difference between quadrats, with the higher values being obtained for the individuals in the quadrats 2.3 and 9.2 which were fairly open. The lowest value was obtained for the individuals in quadrat 6.2 where the sward was quite vigorous and included Kobresia simpliciuscula. The half-life values for the individuals in the other quadrats are in between but with quadrats 3.2 and 3.4 having quite low values. This may, as with quadrat 6.2, have been associated with greater interspecific competition increasing the risk of mortality in the closed grass sward. Results for quadrats 2.2 and 9.3 are lower than might be expected if indeed interspecific competition was important in increasing the risk of mortality. However, quadrat 2.2 was situated in an area periodically disturbed by moles and quadrat 9.3 extremely open, both factors may have helped increase the risk of mortality of individual plants which is suggested by the lower half-life values.

Table a

HALF-LIFE VALUES

Viola rupestris

Quadrat	Half-life (years)	No.
2.2 (disturbed)	9	62
2.3 (± open)	14	38
3.2 (closed)	10	31
3.4 (± closed)	11	20
6.2 (closed)	8	23
9.2 (± open)	16	89
9.3 (open)	11	55

No. - Number of individuals in the originally recorded mixed-age quadrat population

SECTION 4: SEASONAL SURVIVAL AND ANNUAL RECRUITMENT

Seasonal survival over approximately six-monthly periods, (corresponding roughly with the Summer and Winter seasons) varied quite considerably both between quadrat and between season (Table b). The individual values represent the proportion of plants surviving over each period expressed as a rate per individual present at the beginning of each time interval. For this species the number 'at risk' includes all surviving vegetative shoots regardless of their age, together with seedlings which survived one winter period. Further details of the presentation of these figures are given in Chapter three. (Figures are not available for some quadrats in some seasons because the permanent quadrats had not at the time been established).

The lowest single rate of survival occurred during the Summer season of 1970 for the individuals in quadrat 2.3; four of the quadrats by comparison had survival rates of 1.00 in at least one season. Although the rates varied a great deal, the lower seasonal values for each quadrat tended to occur in the same season. When comparisons are made between the overall values for each of the seasons, Summer 1969 and 1970 had rates which are statistically, significantly lower at the 5% level of probability than the other rates, with the exception of that for the Winter period 1968/69. However, this last value is also significantly different at the 5% level from the other values.

By comparison, differences in the overall survival rates show no statistically significant differences at this level of probability between the quadrats. These results suggest that the risk of mortality is increased by seasonal factors operating mainly during the growing season. These probably included interspecific competition, discussed in Section 3

Table b

SEASONAL SURVIVAL

Viola rupestris

QUADRAT

SEASON	2.2 (disturbed)	2.3 (± open)	3.2 (closed)	3.4 (± closed)	6.2 (closed)	9.2 (± open)	9.3 (open)	
Winter 1968/69	0.92	-	0.81	-	-	-	-	0.88 ± 0.03
Summer 1969	0.75	0.84	0.76	-	-	0.85	-	0.82 ± 0.03
Winter 1969/70	0.85	0.95	0.91	-	1.00	0.93	-	0.92 ± 0.02
Summer 1970	0.85	0.72	1.00	0.85	1.00	0.96	0.86	0.88 ± 0.02
Winter 1970/71	0.94	0.94	0.91	0.88	0.90	0.94	0.98	0.94 ± 0.01
Summer 1971	0.99	0.96	0.92	1.00	1.00	0.96	0.79	0.94 ± 0.01
Winter 1971/72	0.99	0.96	0.89	1.00	0.96	0.91	0.91	0.94 ± 0.01
Summer 1972	0.89	0.96	1.00	0.95	0.92	0.95	1.00	0.95 ± 0.01
	0.91 ± 0.01	0.91 ± 0.01	0.90 ± 0.02	0.94 ± 0.02	0.90 ± 0.02	0.93 ± 0.01	0.91 ± 0.02	

Overall seasonal survival for each quadrat population both between quadrat and between season is shown ± standard error

and perhaps other factors such as grazing and the effects of physiological stress on individual plants, brought about by growth and reproduction.

The fact that the seasonal values throughout the period from Winter 1968/69 to Summer 1970 were lower than for the following four seasons, might be related to the lower temperatures experienced in the Winters of 1968/69 and 1969/70 (see Figure 1). These more extreme environmental conditions could well have imposed greater stresses on individuals resulting not only in an increased risk of mortality during these Winter periods but also during the following growing seasons.

By comparison, the Summers of 1971 and 1972 were preceded by Winters in which mean monthly temperatures did not fall below freezing-point and thus stresses imposed on the plants may have been less intense.

Recruitment in Viola rupestris is by the production of underground branches which often give rise to rosettes and by the production of seed, its germination and subsequent establishment of the seedlings. New vegetative shoots appear throughout the growing season and their recruitment to the quadrat populations is expressed as a rate per individual present in the quadrats at the time of the mid-season recording, June to July. Seedlings appear in the Spring and in this case recruitment is expressed as a rate per individual present in the quadrat at that time of year.

The rate of recruitment of new vegetative rosettes into the quadrats varied a great deal (Table c). In two of the quadrats, 3.4 and 9.2, in 1970 and 1969 respectively no new individuals were recorded, whilst quadrat 3.2 had the highest individual value of 0.67 in 1970. Despite this large variation in the individual figures the very high recruitment rate recorded in quadrats 2.2, 2.3, 3.2 and 6.2 in 1970 are a significant

Table c

RATE OF ANNUAL RECRUITMENT OF NEW VEGETATIVE ROSETTES

<u>Viola rupestris</u>

QUADRAT

YEAR	2.2 (disturbed)	2.3 (± open)	3.2 (closed)	3.4 (± closed)	6.2 (closed)	9.2 (± open)	9.3 (open)	
1969	0.09	0.24	0.17	-	0.09	0.00	-	0.09*
1970	0.63	0.40	0.67	0.00	0.33	0.13	0.16	0.30*
1971	0.10	0.04	0.03	0.27	0.25	0.16	0.06	0.11*
1972	0.11	0.13	0.06	0.22	0.22	0.11	0.29	0.14*
	0.19*	0.18*	0.18*	0.15*	0.21*	0.10*	0.16*	

Tables c and d. Figures shown with an asterisk represent the annual recruitment rates for the summed totals of each quadrat and year feature of the results shown in Table c. The overall figure for that year is twice as large as for any of the other years, and perhaps reflects the more favourable climatic conditions experienced in 1970 (see Chapter three).

Differences between the overall recruitment rates for the individuals in each quadrat are less marked and appear to be unrelated to the extent of vegetation cover in the quadrats. Thus quadrat 9.2, which was fairly open, had the lowest overall recruitment of individuals with quadrats 3.4 and 9.3 intermediate values and the other quadrats higher values. These other quadrats include quadrat 6.2 which had a very closed vegetation and quadrat 2.3 which was relatively open.

Seedling recruitment also varied a great deal; however in this case differences were more marked between quadrat than between year. The highest overall recruitment figures occurred in quadrat 2.2 and were, over the four year period, greater than for any other quadrat. The lower overall values occurred in quadrats 3.4, 6.2 and 9.3 with quadrats 2.3, 3.2 and 9.2 having values in between (see Table d).

The higher annual rates of recruitment of seedlings observed for quadrat 2.2 may well be related to the fact that the vegetation was periodically disturbed by moles. Disruption of the turf may have created optimum conditions for seed germination and establishment in the patches of exposed soil. Recruitment rates for quadrats 2.3 and 9.2 which were both relatively open, although the soil was too shallow for moles to be active, were also quite high.

Very low recruitment figures for the individuals in quadrats 3.4 and 6.2 may have been related to the very closed vegetation which could have restricted seed germination. However, in these areas seed production

Table d

RATE OF ANNUAL RECRUITMENT OF SEEDLINGS

<u>Viola rupestris</u>

QUADRAT

YEAR	2.2 (disturbed)	2.3 (± open)	3.2 (closed)	3.4 (± closed)	6.2 (closed)	9.2 (± open)	9.3 (open)	
1969	0.53	0.20	0.00	-	0.04	0.10	-	0.27*
1970	0.25	0.14	0.25	0.00	0.11	0.07	0.02	0.12*
1971	0.12	0.02	0.11	0.06	0.00	0.14	0.00	0.08*
1972	0.11	0.07	0.05	0.00	0.00	0.18	0.00	0.09*
	0.23*	0.15*	0.10*	0.02*	0.05*	0.13*	0.01*	

was very small and the effect of a closed sward on the ability of plants to flower and set seed may have played a more important role in determining these low recruitment figures. As we will see in Section 6, quadrats situated in areas where flowering was prolific were also the quadrats where the seedling recruitment was high.

Quadrat 9.3, however, provides an exception to this conclusion in that although situated in an area where the number of seed set was high it had the lowest overall seedling recruitment. In fact, over the study period only one seedling was recorded in the quadrat. The habitat was very exposed with a patchy cushion-like vegetation and the low germination may have been related to the extreme conditions which might be expected to be experienced at ground level.

Quite large differences are also apparent when comparisons are made between years for the results shown in Table d. Germination in 1969 was much greater than in the other three years and this may well be linked to the much lower mean temperatures experienced in the preceding Winter of 1968/69. Although the seedling recruitment rate for 1970 was not as high nevertheless it was greater than 1971 and 1972. Again the mean air temperature in the preceding Winter 1969/70 was low, dropping below freezing-point in several months in sharp contrast to the Winter periods 1970/71 and 1971/72 when the mean monthly air temperature remained above the freezing-point throughout (see Figure 1). Viola rupestris seed requires chilling before germination can occur and the low rates of seedling recruitment in 1971 and 1972 could be related to the relatively high temperatures in the preceding Winters.

Recruitment to the quadrat populations, both by means of the production of new rosettes and by seed germination and seedling establishment, resulted during the study period in the total number of individuals in each quadrat being maintained, at least at the level of the originally recorded mixed-age population. Overall, vegetative reproduction was of greater significance to the maintenance of the population, with annually 16 new vegetative shoots being produced per 100 individuals in the quadrat populations compared with 13 seedlings.

SECTION 5: AGE-SPECIFIC SURVIVAL AND AGE-DISTRIBUTION

Survival of individuals of known age was independent of the age of the individual. This is indicated by the curves shown in Figure 6 which, with the exception of that for the seedlings which appeared in 1969, all correspond to Deevey (1947) type 2. The linear nature of these curves when plotted on a logarithmic scale implies that for individuals 'born'[*] at the same time there is a constant risk of mortality throughout the life of the individual. Curves are presented for both seedlings summed for all quadrats in each year (continuous line) and for additional vegetative shoots also summed for all quadrats in each year (broken line). During the study period the majority of seedlings appeared in the Spring and therefore the survivorship curves for each age-cohort start at that time. On the other hand new vegetative shoots were recorded throughout the growing season and in order to simplify the graphs <u>all</u> new rosettes appearing in each year are shown as a Summer total.

---

[*] 'Born' is used in this context to indicate that a new individual had been recorded in the quadrat either as a new vegetative rosette or seedling.

The fact that all the curves but one are linear is perhaps surprising, since it might have been expected that seedling mortality would be greater during the initial stages of establishment. However, only seedlings recruited in 1969 showed this pattern of mortality; the survivorship curves for the other seedling groups show that even during the period immediately following germination the rate of mortality is low. Annual weedy species in particular show very high seedling mortality; however this is associated with the production of large numbers of often very light seed. In these species dispersal is all important, enabling exploitation of disturbed areas where interspecific competition is almost non-existent.

Viola rupestris on the other hand has a relatively slow rate of turnover, and a correspondingly low requirement for the recruitment of new individuals. In this species, in addition to the steady replacement by new vegetative shoots, in open areas the production of small amounts of large seed, provides a source of new plants. The survival rate of the relatively large seedlings is high and this is due, in part at least, to the seed size.

The relatively low rate of mortality in this species is emphasised by the large proportion of older individuals present in each quadrat at the end of the study period (Table e). In all but quadrat 2.2, which was situated on the most unstable substrata, approximately half of the individuals present at the end of the study period (Autumn 1972) were surviving members of the original quadrat population.

The table gives a clear indication of the relative importance of the two modes of reproduction to the maintenance of the quadrat populations. Only in quadrat 9.2 was the germination and establishment of

Table e

DISTRIBUTION OF AGE-CLASSES IN EACH QUADRAT
AT THE END OF THE STUDY PERIOD

Viola rupestris

QUADRAT

	AGE IN YEARS	2.2 (disturbed)	2.3 (± open)	3.2 (closed)	3.4 (± closed)	6.2 (closed)	9.2 (± open)	9.3 (open)
Present Autumn 1968	> 4	30	25	16	-	12**	63**	-
'Born' year Aut. 1968-Aut. 1969	3-4	2(4)	3(6)	2(0)	14*	1(0)	0(7)	38*
'Born' year Aut. 1969-Aut. 1970	2-3	16(3)	11(4)	9(4)	0(0)	4(2)	7(5)	1(1)
'Born' year Aut. 1970-Aut. 1971	1-2	6(7)	2(1)	1(4)	4(0)	3(0)	5(10)	2(0)
'Born' year Aut. 1971-Aut. 1972	< 1	8(9)	7(4)	2(1)	4(0)	5(0)	10(19)	12(0)

* Individuals > $2\frac{1}{2}$ years old, first recorded Spring 1970

** Individuals > $3\frac{1}{2}$ years old, first recorded Spring 1969

Figures in brackets represent surviving seedlings; figures not in brackets are surviving vegetative shoots seedlings more important than vegetative reproduction in providing replacement individuals and in this quadrat two thirds of the surviving new plants originated from seed. In quadrat 2.2 there was almost equal emphasis on both forms of reproduction whilst in quadrats 2.3 and 3.2, although seedling recruitment was important, a larger proportion of replacement individuals were from vegetative shoots. Maintenance of the populations in quadrats 3.4, 6.2 and 9.3 was almost entirely dependent on the appearance of new shoots.

In all but quadrat 9.3 the importance of the establishment of seedlings to the survival of Viola rupestris appears to be related to the extent of the vegetation cover. The smaller number of individuals originating as seedlings in quadrats with a closed vegetation may be a direct result of the reduction in the ability of plants to flower and set seed in this type of habitat (see Section 6).

SECTION 6: REPRODUCTIVE PERFORMANCE

The ability of individual plants of Viola rupestris to flower, fruit and set seed is directly related to the density of the vegetation in which they were growing. The rate of production of seeds (potential new plants) for the four different sites selected for this species on Widdybank Fell is shown in Table f.

The highest rate of seed production per 100 plants was observed at site 9 (open), where data were collected from quadrat 9.3 and sample site 9ss3. At this site the plants, which were growing in an extremely open situation, flowered freely. Over the four years for which data are available 33% of the individuals flowered in each year. Many of the plants which flowered went on to produce fruits, mostly from closed flowers.

Of the fairly large number of plants recorded at site 9 (± open) 22% flowered and although in absolute terms the number of flowering plants was higher, in fact fewer fruits were formed. Overall this resulted in a much smaller number of seeds being produced in relation to the total number of plants recorded in this area where the vegetation was more vigorous than at site 9 (open). The results for this site include data from quadrat 9.2 and sample site 9ss2.

At site 2 where the plants were situated in an area where the vegetation was quite vigorous but open, the rate of production of seed was relatively high. As at site 9 (± open) a large number of plants produced a large number of flowering individuals. In this case the number of fruits was also high although when the amount of seed produced is related to the total number of plants recorded it can be seen that the rate of production is approximately the same as for site 9 (± open). The results for site 2 include data from quadrats 2.2 and 2.3 in addition to one sample site 2ss2.

At all three of these sites the density of individuals of Viola rupestris was high and it was possible to sample a fairly large number of plants. Open flowers were quite abundant in these areas although only a relatively small number produced ripe capsules. It is possible that the flower with its relatively long peduncle, which elongates slightly as the fruit develops, may have been eaten by sheep. Closed flowers produced throughout the growing season on Widdybank Fell were recorded in fairly high numbers at these three sites and a large proportion produced ripe fruits. In this case the peduncle was short and not conspicuous

Table f

ESTIMATED SEED PRODUCTION PER 100 PLANTS BETWEEN SITES

<u>*Viola rupestris*</u>

SITE	Total No. plants	No. flowering	Total No. fruits	Mean No. seeds/fruit	No. seeds/ 100 plants
9 open	539	180	78	9.2	123
9 ± open	1,145	251	67		86
2	1,321	232	128	8.4	81
3	627	21	0	0.0	0
6	226	12	0	0.0	0

N.B. Although seeds produced from open flowers may have a very long term effect on the ability of the population to adapt to changes in environmental conditions, as far as being potential replacements to the population in the short term they are of equal importance and have therefore been considered together in Tables f and g until the fruit became erect when ripe, and in this way was probably overlooked by the sheep.

No fruits were recorded from sites 3 or 6 where the vegetation was almost completely closed during the study period. At both these sites only a very small proportion of the plants flowered, 3% and 5% for the sites 3 and 6 respectively. The results include data from quadrats 3.2, 3.4 and sample site 3ss1 for site 3 and quadrat 6.2 and sample site 6ss2 for site 6.

In contrast to sites 9 (open), 9 (± open) and 2 the density of individual plants of Viola rupestris at sites 3 and 6 was low. Very few closed flowers and almost no open flowers were produced. Although no ripe fruits were observed at these sites, seedlings were recorded. This suggests that at some time seed may have been set and remained in a viable state in the soil, or that seed was transported into the area by animal agents such as sheep or man.

Overall, these results show that seed production in Viola rupestris was adversely affected by the proximity of other vegetation. The very low reproductive performance of the plants growing in the closed habitats, where population density was low, suggests that the species may be near the limit of its tolerance in these conditions. This result would seem to confirm the statement made by Valentine and Harvey (1963) that Viola rupestris 'is generally a species of open habitats, and it does not occur in dense shade or where the community is completely closed'.

Differences in the ability of plants to flower and set seed are much less marked when the results are presented so that yearly values can be compared (Table g). By far the greatest number of seeds were produced in 1970 and 1971, and in the first of these years the higher value

Table g

ESTIMATED SEED PRODUCTION PER 100 PLANTS BETWEEN YEARS

Viola rupestris

YEAR	Total No. plants	No. flowering	Total No. fruits	Mean No. seeds/fruit	No. seeds/ 100 plants
1969	1,055	132	44	9*	38
1970	868	188	93	10	107
1971	934	196	111	8	95
1972	1,000	180	65	8	52

* For 1969 few data are available for the number of seeds produced per capsule so an overall mean value for all the years has been used to estimate the total number of seeds produced

may have been related to the more favourable climatic conditions in that year (see Chapter three, Figure 1).

SECTION 7: SPECIES BIOLOGY

Viola rupestris is a perennial species with a relatively high individual longevity. There were no obvious signs of grazing or pulling out by sheep and longevity does not appear to have been affected by the plant flowering. Although a few individuals died after flowering this was the exception rather than the rule and a number of individuals flowered in all four years of the study (Figures 7, 8 and 9). These show the behaviour of the populations in quadrats 3.2, 3.4, 9.2 and 9.3 and clearly illustrate that individuals may flower (broken and dotted line) in more than one year. (After Tamm 1948).

Plants can flower when they are only one year old, although this has only been recorded for plants grown from seed in pots in Durham City, Valentine and Harvey (1963). Under natural conditions in Teesdale up to the end of the study period, at least, only one plant established in the quadrats from a seedling had flowered but this was not until it was four years old. In the same quadrat (2.2) a few vegetative additions had also flowered, one in its second year. The more extreme climatic conditions prevalent in Upper Teesdale appear to restrict the rate of development of individuals, such that the age at which a plant developed from a seedling and possibly a vegetative shoot reaches maturity and flowers, is delayed.

Seed was set in all four years of the study, mainly from fruits developed from closed flowers. Details of the mean number of flowers and fruits from plants producing both open and closed flowers are given in Table h. The mean number of seeds per capsule is also given for capsules produced from closed flowers. Data have been collected for each of the three sites mainly from the permanent quadrats and sample sites as specified in Section 6, although capsules had to be collected from a wider area. (As ripe capsules were relatively infrequent only a small amount of seed was removed from the Fell). Data are not available for sites 3 and 6 as very few plants flowered and none produced capsules.

The mean number of open flowers and fruits from open flowers per flowering plant was much smaller in all seasons and at all sites than the mean number of closed flowers and fruits from closed flowers. Over the four years, only in 1969 was there any appreciable number of open flowers, or fruits from open flowers produced.

When comparisons are made between years, 1969 appears to have been the best year for the production of fruits from both open and closed flowers. The only discernible differences for the results when comparisons are made between quadrats are for the number of open flowers, where the largest number have been produced in all four years at site 2.

Chasmogamous (open) flowers appeared in the latter part of April at Arnside, Valentine and Harvey (1961) and in May at the other two higher sites in Britain, including Upper Teesdale. This flowering was limited to only three or four weeks. Cleistogamous (closed) flowers started to appear in May and continued through the season to September in 1969, 1971 and 1972 on Widdybank Fell and even into October in 1970. On one or two plants, ripe but undehisced fruit from open flowers was present at the same time as young fruits from closed flowers. Fruits from closed flowers were produced from mid-July to mid-August, by which time most had been

Table h
FLOWER, FRUIT AND SEED PRODUCTION
Viola rupestris

YEAR	SITE	Open flowers	Closed flowers	Fruits from:		Seeds/capsule
				Open flowers	Closed flowers	
1969	2	0.78 ± 0.21	1.21 ± 0.28	0.37 ± 0.12	0.53 ± 0.16	No data
	9 ± open	0.30 ± 0.10	1.52 ± 0.30	0.30 ± 0.10	0.87 ± 0.25	No data
	9 open			No record		
1970	2	0.20 ± 0.05	0.67 ± 0.10	0.05 ± 0.03	0.65 ± 0.09	9.97 ± 0.35
	9 ± open	0.02 ± 0.02	0.59 ± 0.10	0.00	0.48 ± 0.09	10.00 ± 0.96
	9 open	0.15 ± 0.05	0.38 ± 0.10	0.06 ± 0.03	0.35 ± 0.07	
1971	2	0.37 ± 0.07	1.34 ± 0.14	0.00	0.69 ± 0.08	7.61 ± 0.34
	9 ± open	0.00	1.35 ± 0.13	0.00	0.51 ± 0.09	9.23 ± 0.52
	9 open	0.06 ± 0.03	1.52 ± 0.16	0.05 ± 0.03	0.41 ± 0.07	
1972	2	0.29 ± 0.06	0.93 ± 0.11	0.00	0.36 ± 0.06	7.61 ± 0.70
	9 ± open	0.09 ± 0.04	1.51 ± 0.18	0.00	0.28 ± 0.05	8.50 ± 0.67
	9 open	0.10 ± 0.04	1.10 ± 0.14	0.04 ± 0.03	0.41 ± 0.09	

N.B. Figures for flower and fruit production are given as a mean per flowering plant ± standard error. The mean number of seeds/capsule is also given ± standard error formed. These fruits can be distinguished from fruits from open flowers by their short peduncle and the absence of a style.

On Widdybank Fell seed germination has been recorded in April and May although most seedlings appeared in May.

Open flowers have been visited by dipterous insects on Widdybank Fell, (personal communication J. Muggleton, 1969), and by Bombus spp. (personal communication M. E. Bradshaw, 1970). The spur was found with bites which were similar to those made in the calyx tube of Gentiana verna by Bombus lucorum. A detailed analysis of the floral biology of Viola riviniana, Viola hirta and Viola reichenbachiana is given in Beattie (1969).

A hybrid between Viola rupestris and Viola riviniana which occurs on Widdybank Fell was not discovered at the other Pennine site where the two species occur together, (personal communication M. E. Bradshaw, 1971) and has not been reported in the literature from any other locality in Europe. The hybrid flowers prolifically, but is sterile, clones of several square metres develop from the soholes (root shoots) a character inherited from the Teesdale Viola riviniana parent. More details of the biology of this species are given in Chapter six.

Dispersal of the seeds of Viola rupestris, which are quite large, would appear to depend on animals. Seeds of Viola spp. have an oily appendage, the elaisome, also found in Polygala spp. which attracts ants that carry the seed away, Ridley (1930). Ants are known to be common on Widdybank Fell and may, as in the case of quadrat 9.3, be responsible for the removal of seeds from the quadrat, thus preventing germination in that quadrat.

Germination has taken place in the Spring both on Widdybank Fell and in Durham. In Durham seed sown in the Autumn germinated the following Spring and it is likely that a long chilling period is necessary. In Viola riviniana seed six weeks' chilling did not produce any germination, Harvey (1962). For successful germination Viola rupestris should be sown outside before November. The cotyledons on the Fell were large, but growth of the seedlings was slow with cotyledons persisting throughout the first growing season.

SECTION 8: LIFE STRATEGY

Viola rupestris is a long-lived perennial species. The present study reveals, when half-life values are calculated from the decay in the number of individuals in the mixed-age populations when each permanent quadrat was set up, that some plants may live for 32 years or longer. Other workers Williams (1970) for Chloris acicularia in ungrazed meadows, Blake (1935) for a number of prairie plants and Robotnov (1960) for Trifolium pratense in sub-alpine meadows have reported life spans for individual plants of some 48, 10-20 and 20 years respectively. By comparison Antonovics (1972) for Anthoxanthum odoratum growing on a zinc mine, found that only a few individuals lived for more than 5 years. Thus individuals of Viola rupestris have a relatively long life when compared with these other perennial species. Even where individuals were growing in very closed turf, which appears to reduce longevity, half-life values indicate that some plants may live for as long as 16 years.

Mortality is a continuing risk throughout the life of the plant and is not affected either by the age of the individual or whether it flowers.

Loss of individuals may be by natural senescence or through uprooting by sheep or humans. Damage caused by sheep and perhaps other animals could lead to mortality although so far this has not been found in the few plants which were observed to be partially eaten. During the present study it was not possible to determine the relative importance of these factors but there was little direct evidence of loss of individuals by uprooting.

The relatively low annual rate of mortality of Viola rupestris which is associated with high longevity, requires a fairly low rate of recruitment to ensure maintenance of the population. Recruitment is by the production of relatively small numbers of vegetative shoots and by ~~the production of relatively small numbers of vegetative shoots and by~~ seed germination, both of which occur over a long period of time. New vegetative shoots were produced at an annual rate of 16 per 100 plants present in the population during the Summer. Seedlings appeared at an annual rate of 13 per 100 plants present in the population during the Spring.

It would appear that this species is a repeating producer. Plants do not usually flower until they are more than 4 years old in the case of individuals established from seedlings, and 2 years for new vegetative shoots except under favourable climatic conditions, such as in lowland Durham. So far the study has not revealed the age at which most recruits first flower; relatively few new plants whether established from seedlings or vegetative shoots had flowered by the end of the four-year study period. However, it is clear that once mature, the plants are able to flower in successive years and presumably produce new vegetative shoots also (Figures 7, 8 and 9). The low seedling recruitment rate is associated in this species with a fairly low annual seed yield (73 per 100 plants), and relatively low risk of mortality during the early stages of seed germination and establishment.

Robotnov (1960) found a very similar life strategy for Trifolium pratense growing in sub-alpine meadows. Here plants did not flower until they were 5 to 10 years old, after which they flowered either in successive years or every 2 or 3 years until some individuals were 20 years old. Here individual longevity was combined with low seed yield and slow replacement, although unlike Viola rupestris there was no form of vegetative reproduction. Polygala amarella (Chapter seven) also has a life strategy similar to that for Viola rupestris and Trifolium pratense, although in this species population turnover is more rapid and seed yield slightly greater.

Differences in the behaviour of the populations in the permanent quadrats gives some insight into the factors controlling the population of Viola rupestris on Widdybank Fell. Clearly the nature of the surrounding vegetation is extremely important to this species which, throughout its range, grows in open habitats on light base-rich soils. As has already been stressed the reproductive ability of the plants is adversely affected when they are present in a closed grass sward. In this habitat plants are widely spaced and few in number. As a result the number of individuals recorded in the quadrats was also quite small, see Figure 8, where the behaviour of the individuals in quadrats 3.2 and 3.4 is shown. From this Figure it can clearly be seen that only a small number of plants flower and that there are few seedlings and relatively few new vegetative shoots.

The behaviour of the individuals in quadrats 2.2 and 9.2 by contrast (Figures 7 and 9 respectively) is entirely different. Here there are a large number of individuals many of which flower, and in both quadrats seedling recruitment is high. It is in these relatively open areas that Viola rupestris appears to be growing under optimum or near optimum conditions. Survival of the plant in the closed sward is precarious and may well in the long term rely on seed being brought into the areas from habitats where seed is set or the occasional plant which flowers and sets seed in these closed habitats.

The overall effect of the close proximity of other species in a closed grass sward appears to be a reduction in the density of individuals. Sagar and Harper (1961) for Plantago spp. in grassland and Putwain and Harper (1970) for Rumex spp. found that grasses played an important part in restricting the population size of plants. Removal of grass species in both cases resulted in an increase in population size. It appears that in Viola rupestris interspecific competition restricts population size by preventing seed production. Without this mode of reproduction the population is unable to expand by exploiting open habitats.

Clearly the survival of this species is closely related to the presence of eroding sugar limestone or areas of turf which are periodically disturbed. For the species to have survived through the forest maximum to the present day open habitats must have existed throughout. Plants can survive in grazed grassland and Turner et al. (1973) suggest that grassland communities were present during the forest maximum. It is possible therefore that Viola rupestris has survived since the late glacial period in habitats similar to those that exist today.

Figure 4

TOTAL POPULATIONS

Viola rupestris

FIGURE 4

TOTAL POPULATION – *Viola rupestris*

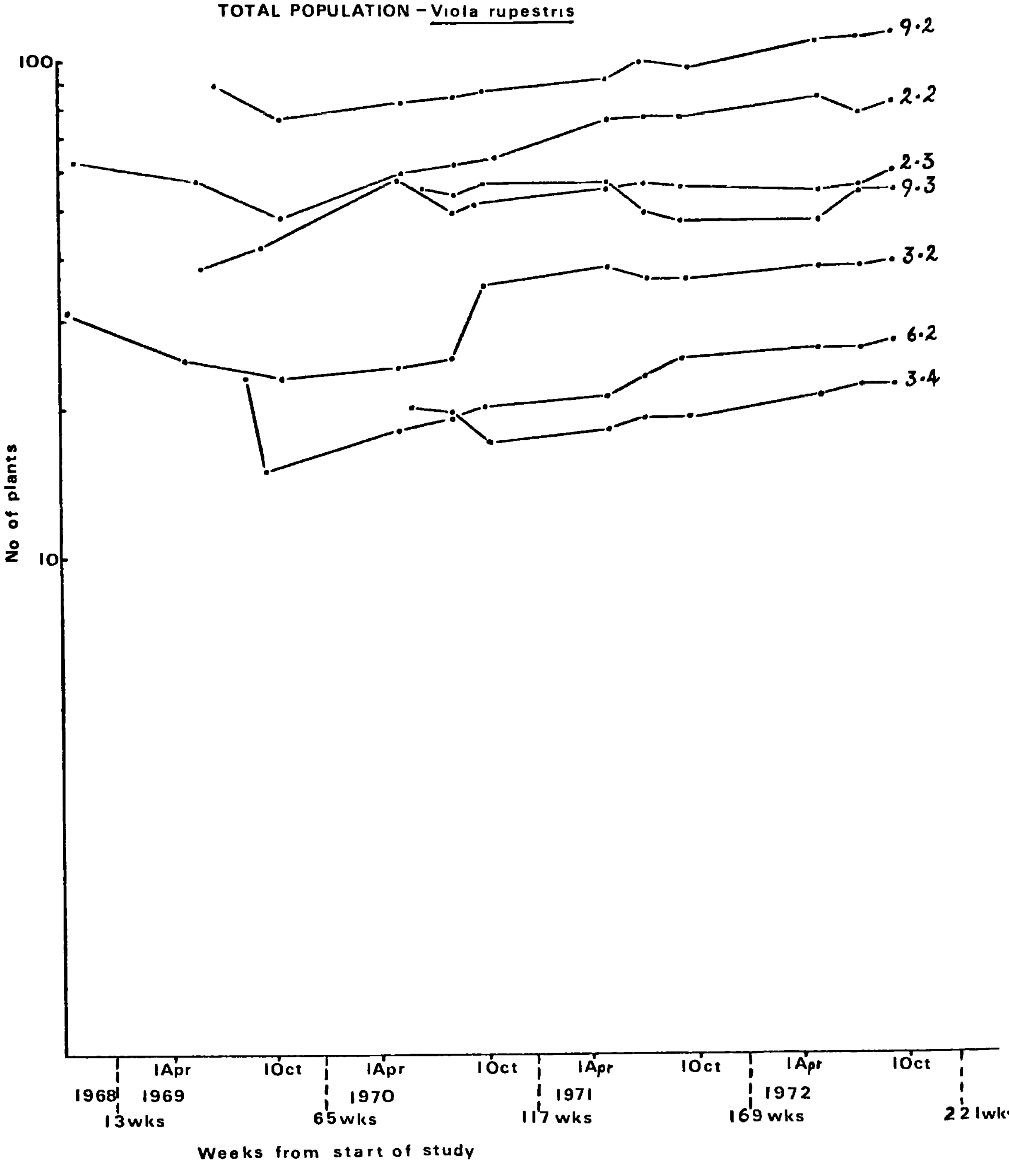


Figure 5

SURVIVORSHIP CURVES OF MIXED-AGE POPULATION

Viola rupestris

FIGURE 5

SURVIVORSHIP curves of mixed age populations-Viola rupestris

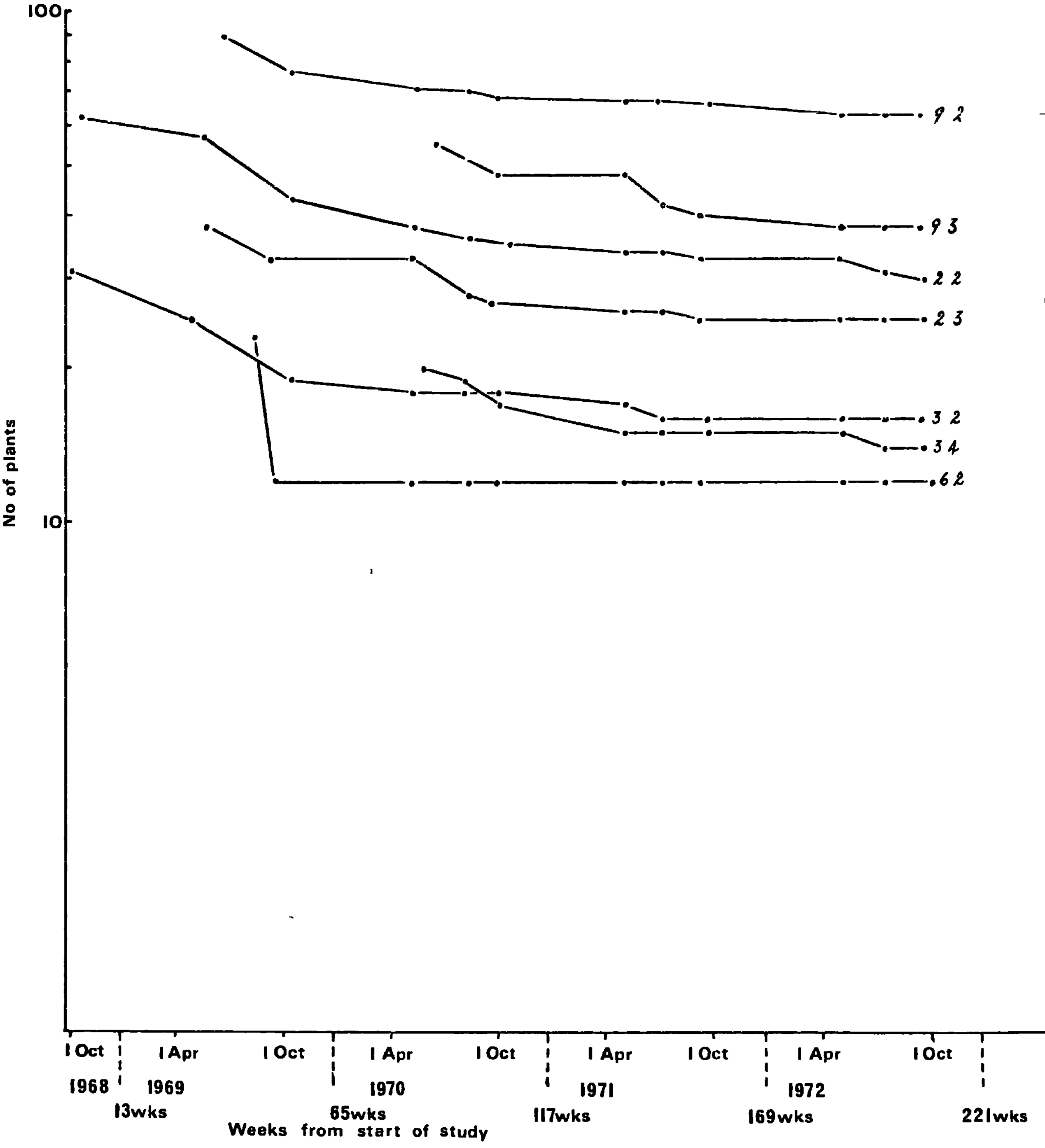


Figure 6

SURVIVORSHIP CURVES OF SEEDLINGS AND
VEGETATIVE SHOOTS 'BORN' AT THE SAME TIME

Viola rupestris

FIGURE 6

SURVIVORSHIP curves of seedlings and vegetative shoots 'born' at the same time –

Viola rupestris

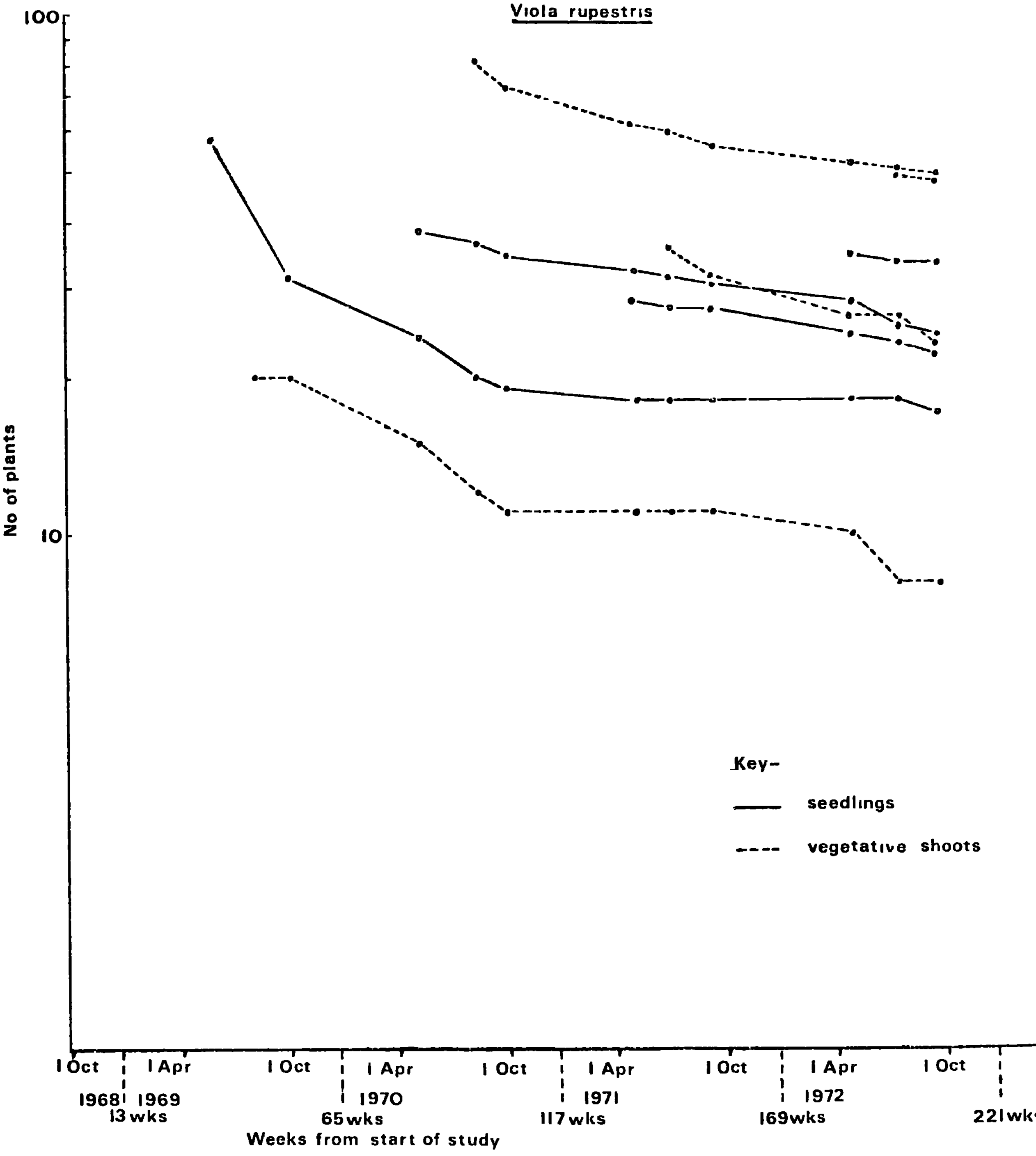


Figure 7

BEHAVIOUR OF INDIVIDUALS IN QUADRAT 2.2

Viola rupestris

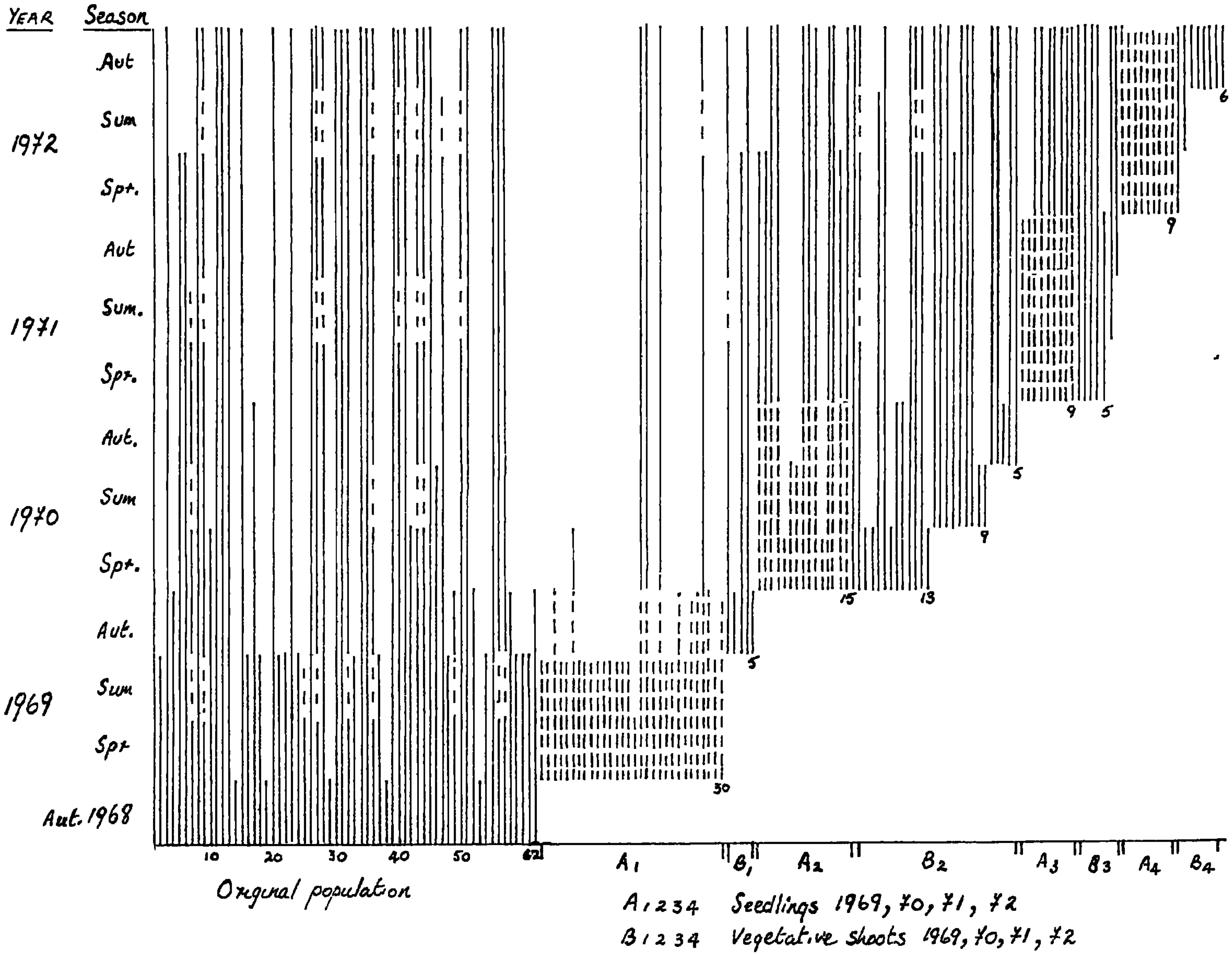


FIGURE 7 Behaviour of individuals in quadrat 2·2 - *Viola rupestris*.

Figure 8

BEHAVIOUR OF INDIVIDUALS IN QUADRATS 3.2 AND 3.4

Viola rupestris

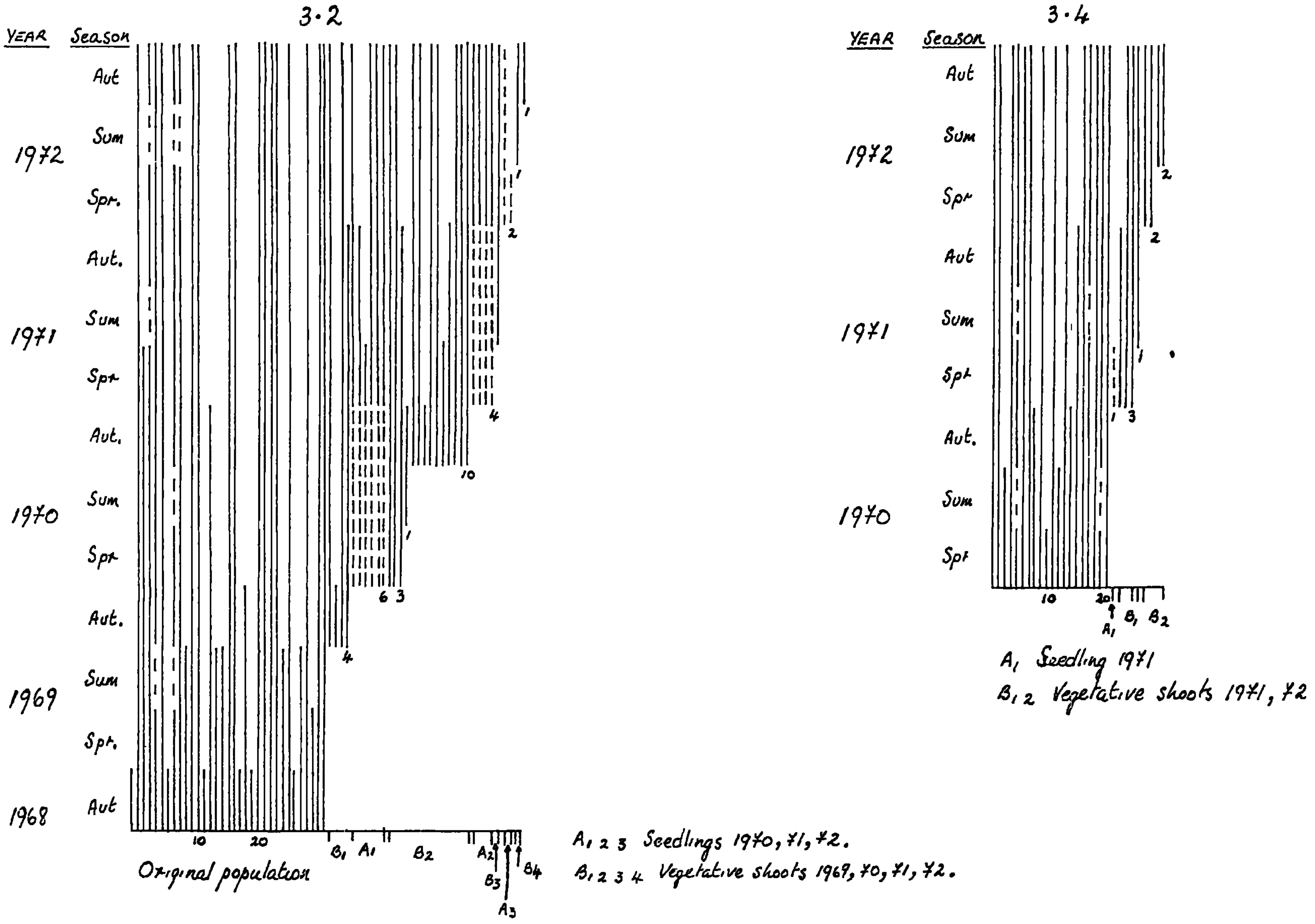


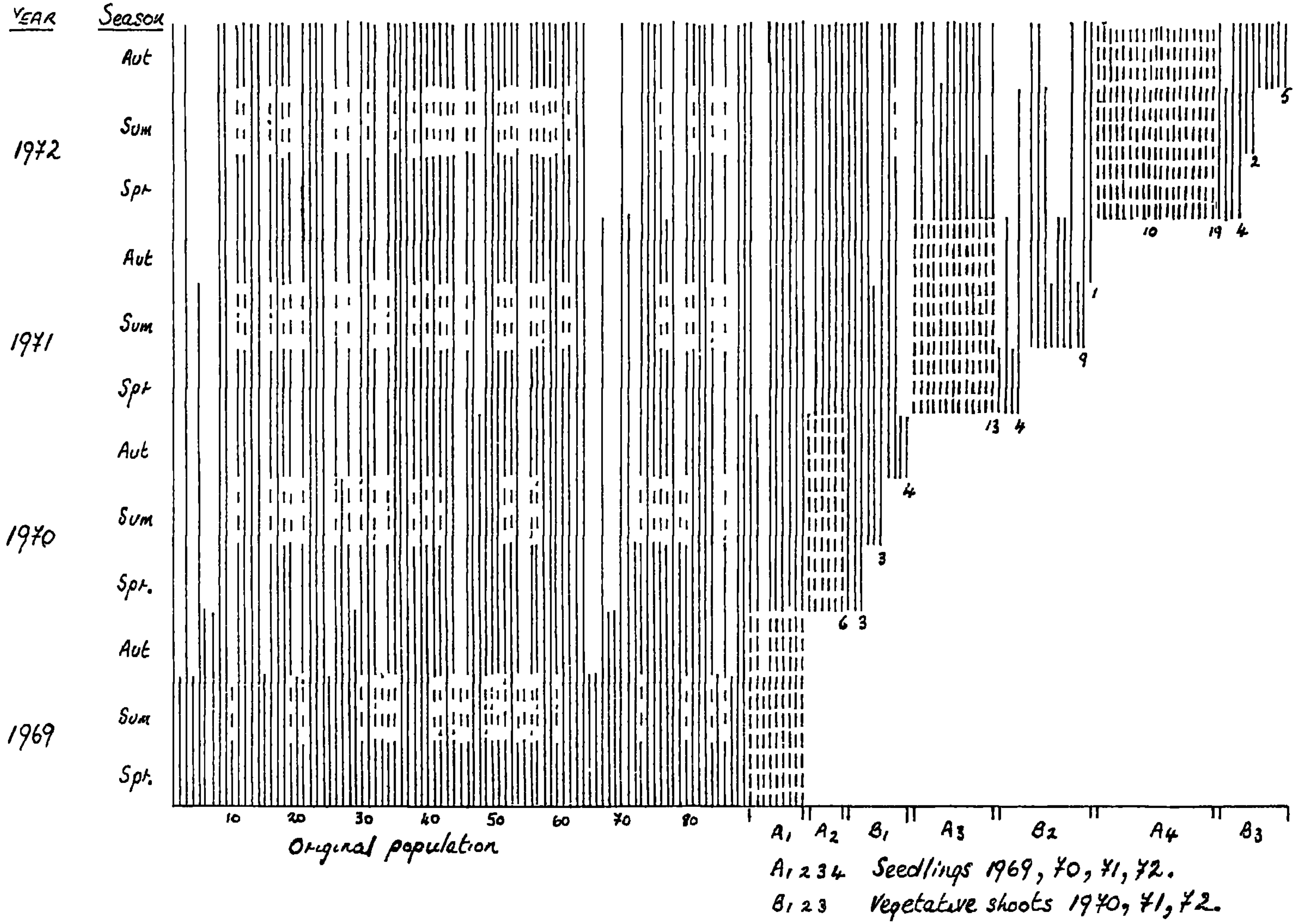
FIGURE 8 Behaviour of individuals in quadrats 3 2 and 3·4 - Viola rupestris

Figure 9

BEHAVIOUR OF INDIVIDUALS IN QUADRAT 9.2

Viola rupestris

FIGURE 9 Behaviour of individuals in quadrat 9·2 - Viola rupestris



CHAPTER FIVE

VIOLA RIVINIANA

SECTION 1: INTRODUCTION

The small rosulate plant, which develops from a seed in Teesdale produces new vegetative shoots from adventitious shoots on the roots (soboles), Valentine (1949). As with Viola rupestris inter-connections of these cannot be ascertained without much damage to the individuals, therefore, the 'unit of reproduction' has been defined as any rosette arising from a seed or underground shoot.

The mature plant, whether it has arisen from a seedling or vegetative shoot, has a short central shoot, a basal rosette of leaves and axillary flowering stems. It is very variable in size (Flora Europaea). It does not seem to produce the short underground branches terminating in rosettes which are found in Viola rupestris.

Longevity is high and replacement of individuals, both by the production of vegetative shoots and by the establishment of seedlings, is correspondingly low. Seed has been set in all four years of the study and the establishment of seedlings plays a significant role in the replenishment of the population, although there are some differences in its relative importance between different sites.

SECTION 2: PERMANENT QUADRATS

Three sites were selected for this species on Widdybank Fell. Site 3 was situated close to the reservoir's edge and here two permanent quadrats were established, one in 1968 and the other in 1970. Sites 6 and 8B were further from the reservoir, the former 200 to 250 metres, the latter over 500 metres from top water-line. *Viola riviniana* was abundant on the sugar limestone soils on Widdybank Fell where *Viola rupestris* was infrequent, particularly in moister areas where there was possibly a thin layer of glacial drift below the soil. *Viola riviniana* itself was only very occasional where *Viola rupestris* was abundant and entirely absent from the open areas of eroding limestone where *Viola rupestris* was dense and flowered prolifically.

Quadrat 3.1 contained a relatively dense cover of *Sesleria caerulea* with *Festuca ovina* and *Kobresia simpliciuscula* and there was little or no bare or moss-covered ground. The vegetation included, in addition, *Helianthemum chamaecistus*, *Antennaria dioica*, *Briza media*, *Carex capillaris*, *Gentiana verna*, *Thymus drucei*, *Plantago maritima* and *Plantago lanceolata*.

Quadrat 3.5 also had a dense vegetation cover dominated by *Festuca ovina* and *Sesleria caerulea*. In this case *Calluna vulgaris* was also present although only sparsely, with *Briza media*, *Botrychium lunarium*, *Plantago lanceolata*, *Thymus drucei*, *Helianthemum chamaecistus*, *Potentilla erecta*, *Koeleria gracilis*, *Viola ~~tricolor~~ lutea* and a little *Kobresia simpliciuscula*.

Quadrat 6.1 was dominated by *Sesleria caerulea* and *Festuca ovina* but with some moss/lichen cover. *Helianthemum chamaecistus*, *Thymus drucei*, *Selaginella selaginoides*, *Briza media*, *Kobresia simpliciuscula*, *Campanula* *rotundifolia* were present together with *Potentilla crantzii* and *Antennaria dioica*. *Polygala amarella* was also recorded in this quadrat (see Chapter seven).

Calluna vulgaris and *Empetrum nigrum* were present in quadrat 8B.2 which otherwise contained a closed sward of *Sesleria caerulea* and *Festuca ovina*. *Gentiana verna*, *Thymus drucei*, *Briza media*, *Selaginella selaginoides*, with occasional *Polygonum viviparum*, *Anemone nemorosa* and *Linum catharticum* were also present. Unusually *Viola rupestris* was also found here, although only in very small numbers.

SECTION 3: POPULATION FLUX

The total number of individuals in each quadrat increased over the period of recording (Figure 10). In the case of quadrat 8B.2 the increase in the originally recorded mixed-age population in Autumn 1968 over the study period was almost 100%. Increases of 20%, 24% and 40% were recorded for the original populations in quadrats 3.1, 3.5 and 6.1 respectively.

This rise in the total population was more pronounced during 1969 and 1970 for quadrats 6.1 and 3.1 and was followed by a levelling-off during 1971 and 1972. The population in quadrat 3.5, which was not established until Spring 1970, remained relatively stable throughout, although there was a slight increase in 1970. In the case of quadrat 8B.2 which showed the greatest increase in numbers the change was gradual and occurred throughout the period from Autumn 1969 to Autumn 1972. Unlike the other quadrat populations there was no indication of stabilization in 1972.

These curves clearly illustrate the stable nature of the population of Viola riviniana on Widdybank Fell, with recruitment being able to make up for the loss of individuals. The upward trend in numbers may be related to the relatively mild climatic conditions which were experienced during a large part of the study period.

The rate of survival of the individuals within each quadrat was high and is indicated by the very shallow nature of the survival curves for the originally recorded quadrat populations shown in Figure 11. Half-life values based on the decay of this original quadrat population indicate that complete replacement of the population may occur every 22 to 66 years (Table a). However, the highest half-life value of 33 years was obtained for the individuals in quadrat 3.5, which was only observed over a 2½ year period when mortality was quite low for all quadrats and is therefore probably exceptional. A more realistic estimate of the time taken for complete replacement of the population is approximately 25 years.

The survival curves of the originally recorded mixed-age population are not only very shallow but also linear. The shallow nature of these curves has already been discussed in terms of half-life values. However, in addition to the fact that the rate of mortality was relatively low, it would also appear that it was constant, at least over the period of recording. The linear nature of the curves, which are similar to Viola rupestris and Viola rupestris x riviniana, conform to Deevey (1947) type 2. These curves with numbers plotted on a logarithmic scale indicate that mortality is a continuing risk throughout the plant's life, that is, mortality is independent of the age of the individual.

Table a

HALF-LIFE VALUES

Viola riviniana

Quadrat	Half-life (years)	No.
3.1	11	40
3.5	33	76
6.1	11	35
8B.2	14	93

No. - Number in the originally recorded
mixed-age population

SECTION 4: SEASONAL SURVIVAL AND ANNUAL RECRUITMENT

Seasonal survival over approximately six-monthly periods was in general lower in the first year and a half of recording (Table b). Large differences can be seen between the values similar to those found for Viola rupestris, ranging from 0.80 over the period Spring 1969 to Autumn 1969 in quadrat 6.2 to 1.00 (that is, no mortality) over the period Spring 1970 to Autumn 1970 in the same quadrat. In this species the number of individuals 'at risk' at the beginning of each time interval is considered to be all individuals in each quadrat excluding first year seedlings.

The lowest survival rates were recorded during the Summer of 1969, and the overall figure is statistically significantly different at the 5% level of probability when compared with the figures obtained for the seasons from Summer 1970 to Summer 1972. The other low values, for the Winter period 1968/69 and Winter 1969/70 are not statistically significantly different at this level of probability from the Summer 1969 figure. However the Winter 1968/69 value is significantly lower than all but the Winter 1971/72, and the Winter 1969/70 value is significantly lower than Summer 1970, Winter 1970/71 and Summer 1972.

It is clear from these figures that mortality was greater during the period from Autumn 1968 to the Winter 1969/70. The lower survival figures during this period may be related to the more severe weather conditions experienced in the Winters of 1968/69 and 1969/70, when the mean daily air temperature was much lower than in the two following Winter periods. These figures are very similar to those obtained for Viola rupestris except for the Summer season 1970 when the survival rate was greater for individuals of Viola riviniana.

Table b

SEASONAL SURVIVAL

<u>Viola riviniana</u>

QUADRAT

SEASON	3.1	3.5	6.1	8B.2	
Winter 1968/69	0.83	-	0.86	0.96	0.90 ± 0.02
Summer 1969	0.82	-	0.80	0.89	0.86 ± 0.03
Winter 1969/70	0.93	-	0.92	0.92	0.92 ± 0.02
Summer 1970	0.98	0.96	1.00	0.96	0.97 ± 0.01
Winter 1970/71	0.98	0.97	0.98	0.96	0.97 ± 0.01
Summer 1971	0.98	0.94	0.98	0.97	0.96 ± 0.01
Winter 1971/72	0.96	0.97	0.96	0.91	0.94 ± 0.01
Summer 1972	0.98	0.98	0.98	0.98	0.98 ± 0.01
	0.94 ± 0.01	0.96 ± 0.01	0.94 ± 0.01	0.96 ± 0.01	

Overall seasonal survival for each quadrat population both between quadrats and between season is shown ± standard error

No data are available for quadrat 3.5 for the first three seasons as it was not established until Spring 1970

Recruitment in Viola riviniana was both by means of new vegetative shoots arising from root shoots and by the establishment of seedlings. New vegetative shoots appeared throughout the growing season and thus their recruitment is expressed as a rate per individual present in the quadrat at the time of the mid-season recording (Table c). As with Viola rupestris seedlings appeared in the Spring and in this case recruitment is expressed as a rate per individual present in the quadrat in the Spring (Table d).

Variation in the rate of recruitment of new vegetative shoots was large, ranging from 0.02 in 1972 to 0.40 in 1969 for the individuals in quadrat 6.1. Unlike the results for Viola rupestris, where the rate of recruitment of vegetative shoots was particularly high in 1970 and low in the other years, in this species recruitment was high in both 1969 and 1970. In quadrat 8B.2 recruitment was high in all years although for the other quadrats it was low in 1971 and 1972. It is clear from Table e that differences in recruitment rates were greater between years than between the quadrats suggesting that climate may be important in determining shoot production.

Seedling recruitment also varies a great deal with rates ranging from 0.00 to 0.27. Overall the figures show that seedlings appeared in greatest numbers in 1969 and 1970 whilst in 1971 and 1972 recruitment was very low, particularly in 1972 when only 3 seedlings were recorded, (Table d).

Differences between quadrats are marked with relatively high rates of recruitment recorded for the individuals in quadrat 8B.2 and low values for quadrats 3.1, 3.5 and 6.1. Data are not available for quadrat 3.5 in 1969 and no seedlings were recorded in 1970 when recruitment in the other quadrats was high, and as a result the overall figure for that quadrat population was very low. There was little difference between the

Table c

ANNUAL RECRUITMENT OF NEW VEGETATIVE SHOOTS

Viola riviniana

QUADRAT

YEAR	3.1	3.5	6.1	8B.2	
1969	0.37	-	0.40	0.11	0.22*
1970	0.31	0.20	0.38	0.22	0.25*
1971	0.06	0.11	0.06	0.20	0.13*
1972	0.04	0.10	0.02	0.24	0.14*
	0.17*	0.13*	0.18*	0.20*	

* Figures shown with an asterisk represent the annual recruitment rates for the summed totals of each quadrat and year

Table d

ANNUAL RECRUITMENT OF SEEDLINGS

Viola riviniana

QUADRAT

YEAR	3.1	3.5	6.1	8B.2	
1969	0.12	-	0.03	0.16	0.13*
1970	0.14	0.00	0.10	0.27	0.15*
1971	0.00	0.01	0.02	0.14	0.07*
1972	0.00	0.01	0.00	0.01	0.01*
	0.06*	0.01*	0.04*	0.13*	

* Figures shown with an asterisk represent the annual recruitment rates for the summed totals of each quadrat and year

vegetation cover in these quadrats and it is difficult to link seedling recruitment with interspecific competition as it was possible to do for Viola rupestris.

SECTION 5: AGE-SPECIFIC SURVIVAL AND AGE DISTRIBUTION

Survival of vegetative shoots of known age appears to be independent of the age of the individual. As with the survivorship curves for the originally recorded mixed-age populations (Figure 11) these curves, shown by a dotted line in Figure 12, are also linear. This again indicates that there was a constant rate of decay and that the risk of mortality was independent of the age of the individual shoots. As there were relatively few new vegetative shoots produced in any one season those that were recorded in the quadrats have been summed and expressed as a single figure for each year. Since the majority of shoots appeared in the Summer, the figure appears as a Summer total on the graph.

The very shallow nature of the curves also shows that mortality of individual new shoots was low. In addition there was little difference in the rates of mortality between groups of individuals 'born'* at the same time, the curves having approximately similar slopes.

Survival of plants developing from seedlings is also independent of the age of the individual. The linear nature of the curves, which

---

* 'Born' is used in the same context as for Viola rupestris, that is, it refers to the appearance of new individuals in the quadrats whether vegetative shoots or seedlings

show the decay in the number of plants first appearing as seedlings (continuous line in Figure 12) in the Spring of each year, indicates that there is a constant risk of mortality throughout the early stages of the plant's life.

The curve for the seedlings first appearing in 1971 is the only one which shows any departure from a straight line. Although all the other curves approach Deevey (1947) type 2, the curve for the 1971 seedlings, on the other hand, approaches Deevey (1947) type 1. Curves of this kind indicate that mortality is not independent of the age of the individual, but that there is a greater risk of an individual dying in the early stages of its life. In the case of plants developing from seedlings, the stage when this risk is greatest is during the initial phases of seedling establishment. The fact that only one group of seedlings showed this increased mortality suggests that the result may be exceptional. The relatively large seed size of Viola riviniana as with Viola rupestris probably helped reduce the risk of mortality during this critical phase of the plant's life.

A very large proportion of the individuals in the quadrats were mature plants, that is, those surviving from the originally recorded mixed-age population (see Table e, where the distribution of age classes in the Autumn of 1972 is shown for each quadrat). This fact reflects the relatively high longevity of individuals as indicated by the shallow nature of all the survivorship curves (Figures 11 and 12) and by the high half-life values (Table a).

Quadrat 8B.2 was exceptional in that approximately three quarters of the population present in the Autumn of 1972 was made up of plants 'born' during the study period. Quite a high proportion of the new

Table e

AGE-DISTRIBUTION OF PLANTS WITHIN EACH QUADRAT - AUTUMN 1972

<u>Viola riviniana</u>

		QUADRAT			
	AGE IN YEARS	3.1	3.5	6.1	8B.2
Present Autumn 1968	> 4	22	No record	19	58
'Born' year Aut. 1968-Aut. 1969	3-4	8(3)	No record 67*	10(1)	7(12)
'Born' year Aut. 1969-Aut. 1970	2-3	11(2)	11(0)	11(3)	19(21)
'Born' year Aut. 1970-Aut. 1971	1-2	0(0)	6(1)	3(1)	21(11)
'Born' year Aut. 1971-Aut. 1972	< 1	2(0)	9(1)	1(0)	36(2)

* Individuals > $2\frac{1}{2}$ years olf, first recorded Spring 1970

Figures in brackets represent surviving seedlings; figures not in brackets are surviving vegetative shoots plants arose as a result of seed germination and establishment. In the other quadrats no more than half the quadrat populations in Autumn 1972 were made up of new individuals and of these new plants only a small proportion appeared as seedlings.

The large contribution to the replacement of the population made by seedlings in quadrat 8B.2 may well be related to the slightly more sheltered nature of the quadrat, which was situated in an area which had a high proportion of heather. In the next section it will be seen that it was here that seed production was high and clearly this could be related to the less extreme conditions, which would in turn provide more favourable conditions for seed germination and establishment.

One interesting feature of the results is the very small contribution made by plants developing from seedlings to the maintenance of the populations in the two quadrats at site 3. It was at this site that *Viola rupestris* produced few flowers and very few seedlings. However, unlike *Viola rupestris*, the density of *Viola riviniana* was high and thus the effect of interspecific competition at this site may be solely to restrict the ability of plants to flower and set seed (Section 6).

SECTION 6: REPRODUCTIVE PERFORMANCE

Reproductive performance is discussed in this section in terms of the number of potential new plants~~,~~ and seeds, produced per 100 plants in the populations. Although *Viola riviniana* reproduces vegetatively as well as sexually, it was not possible to record the number of root-shoots, potential new vegetative plants, without destroying the plants in the quadrats.

The differences in seed production between the sites were very marked (Table f). The table shows the total number of plants present at each site, the number flowering, the number of fruits and the mean number of seeds per capsule. From these data an estimate of the actual number of seeds produced per 100 plants in the three areas had been made.

At site 3 data were collected from quadrats 3.1 and 3.5 and from sample site 3ss3; at site 6 from quadrat 6.1 and sample site 6ss1; and at site 8B from quadrat 8B.2 and sample site 8Bss2. These data have been re-calculated to show differences in reproductive performance between years (Table g).

Clearly the greatest differences in seed production occurred between sites with the individuals at site 8B producing annually almost one seed for every plant present in the population. Seed production at the other two sites was much lower with one seed being produced for approximately every 5 plants in the population. This much higher rate of seed production at site 8B suggests that the plants were growing under more favourable conditions than at the other sites. Here the quadrat and sample site were situated in an area with a high proportion of *Calluna vulgaris* which may have helped create a favourable microclimate in which *Viola riviniana* can flower and set seed more easily. The presence of *Kobresia simpliciuscula* in a heavily grazed closed turf at the other two sites may have had the opposite effect by causing increased interspecific competition.

Differences in seed production for each of the years (Table g) were less marked, suggesting that climatic/seasonal variation, at least over the four years of the study, was less important in determining the ability of plants to flower and set seed than the habitat in which the plants were growing. Whether the higher values observed in 1970 and

Table f

ESTIMATED SEED PRODUCTION BETWEEN SITES

Viola riviniana

SITE	Total No. Plants	No. flowering	No. fruits produced from:		Mean No. Seeds/capsule	Estimated No. Seeds/100 plants
			Open flowers	Closed flowers		
3	799	74	3	23	8.7	28
6	621	28	0	13	9.1*	19
8B	1,241	186	4	121	9.6	97

* Because of the relatively small number of capsules produced at site 6, the number of seeds per capsule used in estimating the production of seeds per 100 plants at that site is the mean of all the data collected during the study

Table g

ESTIMATED SEED PRODUCTION BETWEEN YEARS

Viola riviniana

YEAR	Total No. Plants	No. flowering	No. fruits produced from:		Mean No. Seeds/capsule	Estimated No. Seeds/100 plants
			Open flowers	Closed flowers		
1969	589	34	1*	18*	9.1*	29
1970	623	82	5	37	10.0	67
1971	670	82	1	37	8.7	49
1972	779	90	0	62	9.1	72

* Full data are not available for 1969, therefore, the values used in estimating the number of seeds produced in that year are based on the data obtained for the other three years

1972 were related to temperature, rainfall, or differences in the stocking rate of sheep on Widdybank Fell is impossible to determine.

Both open and closed flowers were produced by plants of *Viola riviniana* on Widdybank Fell and fruits from both types of flower were recorded. However, it is apparent from Tables f and g that few fruits were formed from open flowers. Although the production of fruits from this type of flower may be extremely important to the long term survival of the species under changing environmental conditions, in the short term seeds from fruits of open and closed flowers were equally important in providing potential replacement individuals. For this reason the estimate of the number of seeds per 100 plants includes fruits from both open and closed flowers.

SECTION 7: SPECIES BIOLOGY

The results of this study reveal that *Viola riviniana* is a relatively long-lived plant in Upper Teesdale with age-independent mortality. Reproduction which is both by means of the production of new vegetative shoots and by the establishment of seedlings, is correspondingly low. Longevity does not appear to be affected by a plant flowering (Figures 13 and 14). In these figures, where the behaviour of the populations in quadrats 3B.2, 3.1 and 3.5 are shown, each line represents a single plant. A few plants died immediately after flowering (broken and dotted line) but over the study period this involved only 6 individuals. More usually plants survived and often flowered again; one plant flowered in all four years of the study and 8 plants flowered in three of the four years.

A few new individuals flowered in their third year and this was true for plants arising both as a result of vegetative reproduction and by the germination of seed and its establishment. However, this only happened in quadrat 8B.2; in the other quadrats no additional new plants flowered. This again suggests that it was in this area (site 83) that conditions were favourable to plant growth.

Seed was set in all four years of the study both from open and closed flowers.

Chasmogamous (open) flowers appeared on Widdybank Fell in the latter part of May and the first week of June in both 1969 and 1970. In 1971 and 1972 flowers appeared by the second week in May. Open flowers were normally produced over a period of approximately 3 weeks and during this time buds which developed into closed flowers were observed.

Plants transplanted from Upper Teesdale to the University of Durham and grown in tubs flowered 2 to 3 weeks earlier than Teesdale plants growing 'in situ'. The plants also flower for a longer period producing ripe fruits from closed flowers up to the end of September. In the middle of the season flowers were observed which never became fully open. These semi-cleistogamous flowers were produced after the fully open flower and had only very small petals.

Seed germination occurred in the Spring of each year on Widdybank Fell; at the end of May to the beginning of June in 1970 and in the second and third week in May in 1971 and 1972.

A hybrid of this species with Viola rupestris is present on Widdybank Fell (Chapter six).

The production of flowers, fruits per flowering plant and the number of seeds per capsule varies considerably (Table h). The production of open flowers in all but one case was much lower than closed

Table h

FLOWER, FRUIT AND SEED PRODUCTION

(MEAN FLOWERS AND FRUITS PER FLOWERING PLANT; MEAN SEEDS PER CAPSULE)

Viola riviniana

YEAR	SITE	Open flowers	Closed flowers	Fruit from: Open flowers	Fruit from: Closed flowers	Seeds/capsule
1969	3	No record		No record		No record
	6	No record		No record		No record
	8B	0.40 ± 0.09	1.30 ± 0.15	No record		No record
1970	3	0.54 ± 0.11	0.72 ± 0.24	0.12 ± 0.06	0.23 ± 0.10	10.00 ± 0.60
	6	No data		0.00	0.40 ± 0.24	No data
	8B	0.28 ± 0.06	0.78 ± 0.12	0.04 ± 0.03	0.58 ± 0.10	No data
1971	3	0.44 ± 0.16	1.78 ± 0.42	0.00	0.28 ± 0.14	8.24 ± 0.60
	6	0.13 ± 0.13	1.63 ± 0.56	0.00	0.13 ± 0.13	No data
	8B	0.25 ± 0.06	2.02 ± 0.20	0.02 ± 0.02	0.55 ± 0.08	9.13 ± 0.53
1972	3	0.52 ± 0.14	0.41 ± 0.14	0.00	0.41 ± 0.14	7.93 ± 0.60
	6	0.21 ± 0.14	0.93 ± 0.12	0.00	0.71 ± 0.16	No data
	8B	0.16 ± 0.03	0.86 ± 0.09	0.00	0.84 ± 0.10	10.10 ± 0.52

Figures for flower and fruit production are given as a mean per flowering plant ± standard error. The mean number of seeds/capsule is also given ± standard error flowers per flowering plant although there is no indication that any one year was more favourable than any other. By contrast a much greater number of closed flowers were produced at all sites in 1971, with lower values in 1970 and 1972. Differences in the values between sites are also apparent in Table h with the mean number of open flowers per flowering plant slightly greater at site 3 than at the other two sites.

The production of fruits from open flowers was very low with only 17 capsules being recorded in the permanent quadrats and sample sites throughout the study period. The mean number of fruits from closed flowers was very much higher in all years and at all sites, with the greatest number per flowering plant being produced at site 8B in all three years for which full data are available. Unlike the results for the production of closed flowers there is no indication that any season was more favourable than another. This suggests that climatic factors, where they affected reproductive ability, did so only by affecting the production of closed flowers.

The data for the mean number of seeds per capsule were collected from fruits from closed flowers and show that the production of seeds was greater at site 8B. The fact that a greater number of fruits per flowering plant and seeds per capsule were produced at this site is reflected by the figure for reproductive performance at this site given in Section 6, Table f.

Dispersal of the seed was restricted as far as could be ascertained, to the distance from the plant that the explosive mechanism was able to throw the seed. The relatively heavy seed does have an oily appendage which is said to attract ants as in <u>Viola rupestris</u> and <u>Polygala amarella</u>, Ridley (1930) and dispersal may be affected over greater distances.

The seedling, on germination, had large cotyledons, growth was slow and only 2 to 4 leaves were produced during the first growing season. The cotyledons remained visible throughout the period, eventually dying toward the end of the Autumn.

Effective reproduction was both by the production of vegetative shoots and by the establishment of seedlings. The former contributed more to the maintenance of the quadrat populations at sites 3 and 6, whilst both were equally important at site 8B. This distinction is clearly illustrated by Figures 13 and 14 which show the behaviour of the quadrat populations at sites 3 and 8B.

SECTION 8: LIFE STRATEGY

Viola riviniana is a long-lived perennial species. The present study reveals that individual plants may live for as long as 22 years or more (Section 3). This value is of the same order as that obtained in this study for *Viola rupestris* and *Viola rupestris x riviniana* but is lower than that indicated by half-life values calculated by Harper (1967) for *Filipendula vulgaris* and *Sanicula europaea* from data given by Tamm (1956b). For these species it appears that individual plants may live for as long as 36 years and even up to 100 years respectively.

Mortality was a continuing risk throughout the life of the individual and was not affected either by its age or whether it flowered. Some individuals were affected by animals but there was no direct evidence of any having been lost directly as a result of damage or uprooting by grazing.

The relatively high longevity of individual plants within the permanent quadrats requires only a correspondingly slow rate of recruitment to ensure survival of the population. Thus an annual mortality of 13 plants per 100 in the population was made up by recruitment of vegetative shoots and seedlings at rates of 16 and 8 plants per 100 respectively. Those figures clearly show that the number of individuals recruited to the population was greater than the number that were lost. This fact combined with the low rates of mortality for the new individuals led, over the study period, to an increase in the total population within each of the quadrats.

Twice as many new plants appeared as a result of vegetative reproduction than by seed germination and establishment of seedlings. Thus the population could probably be maintained entirely by vegetative reproduction, although the species would be unable to adjust genetically to changes in environmental conditions. However, even the sexual reproductive mechanism is almost totally inbreeding with ripe seed being produced mainly from closed flowers. A very few ripe capsules were produced from open flowers and it must be from this outbreeding mechanism that new genetic combinations arise and allow the population to adjust to environmental change. Thus, although the production of vegetative shoots and of seed in fruits from closed flowers was important to the short term survival of the species, the long term survival will depend on the ability of the population to produce ripe fruits from open flowers.

The production of potential new plants (seeds) was relatively high, almost attaining an annual rate of one seed per plant in the population. This compares with the actual recruitment of seedlings which, over the study period, ran at a rate of 8 per 100 plants in the total population. Thus, annually, only approximately 8% of the potential new plants (seeds) actually germinated and entered the population as seedlings. The remaining 92% of the seed either lay dormant in the soil, was destroyed or may have been carried out of the quadrats to germinate elsewhere. It is known that the rate of germination in _Viola rupestris_ is very low and it is likely that this is also true for _Viola riviniana_.

As with _Viola rupestris_, this species is a repeating producer. Plants will flower in their third year and once mature are capable of producing flowers and fruits in successive years. Recruitment of both vegetative shoots and seedlings is low and the risk of mortality of these individuals is on the whole no greater than for mature plants. The longevity of individuals of this species is associated with relatively low seed yield, producing approximately one seed per individual in the population per annum, and slow replacement.

Figure 10

TOTAL POPULATIONS

Viola riviniana

FIGURE 10

TOTAL POPULATION - *Viola riviniana*

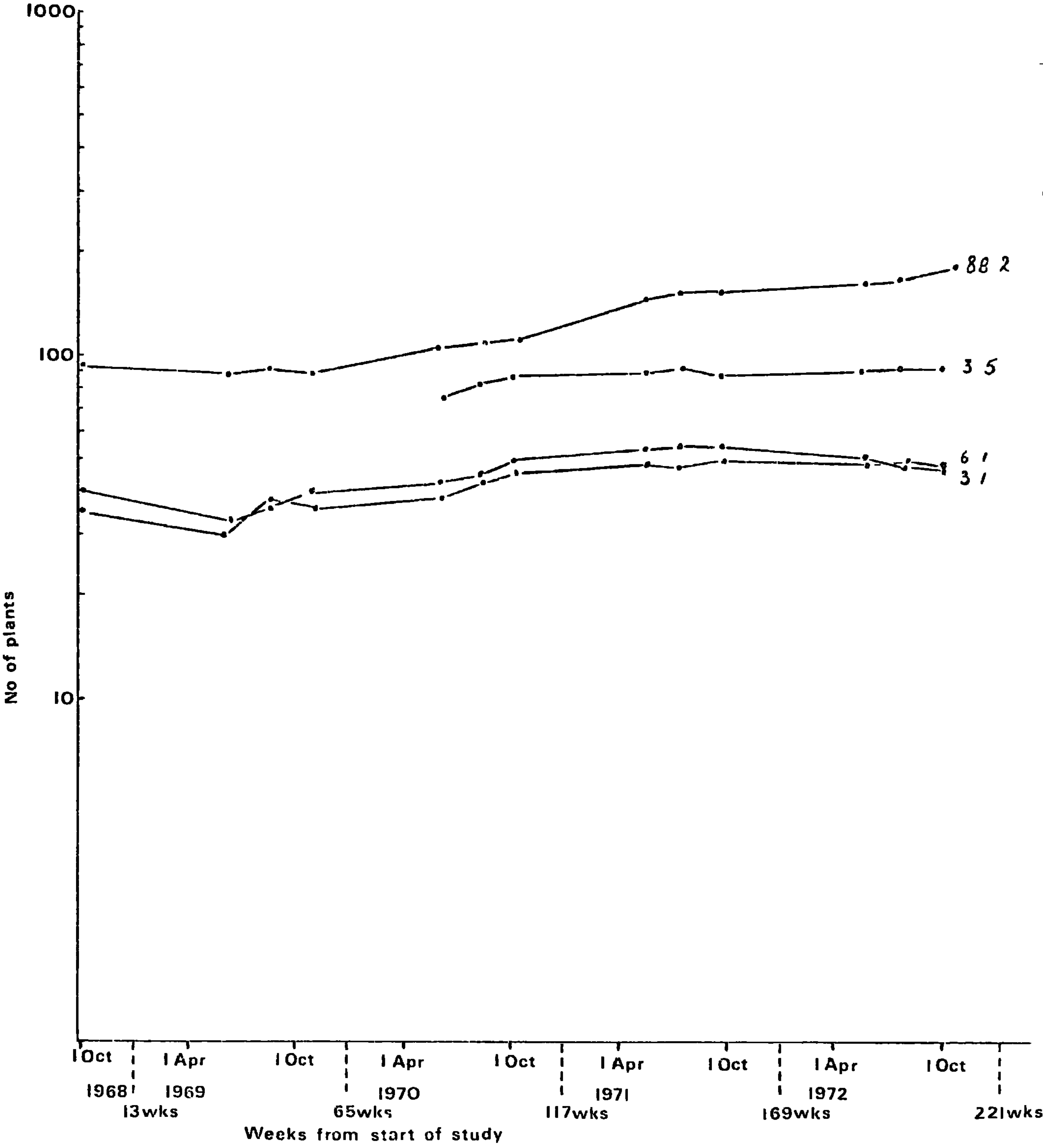


Figure 11

SURVIVORSHIP CURVES OF MIXED-AGE POPULATION

Viola riviniana

FIGURE II

SURVIVORSHIP curves of mixed-age populations-Viola riviniana

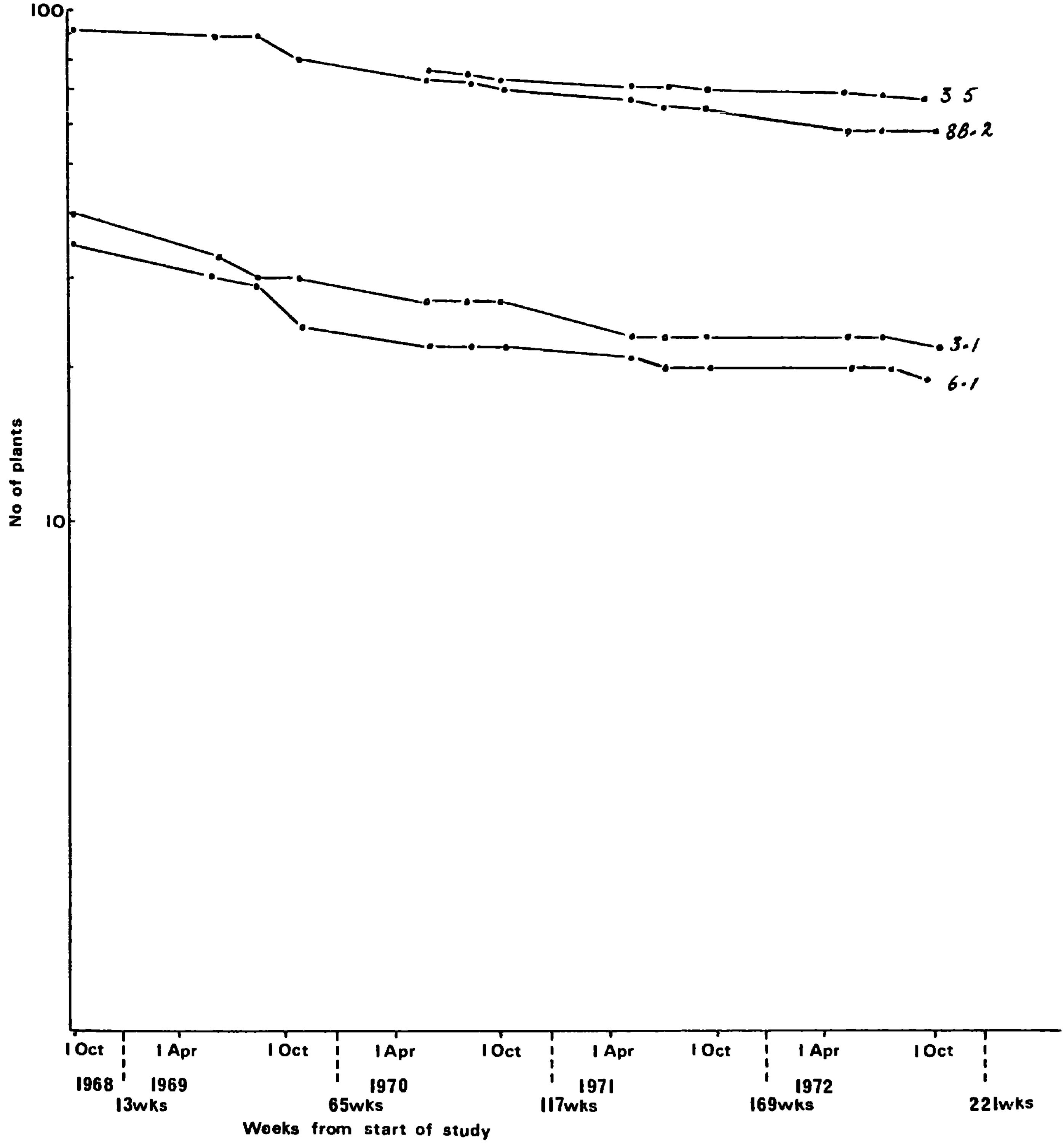


Figure 12

SURVIVORSHIP CURVES OF SEEDLINGS AND VEGETATIVE SHOOTS 'BORN' AT THE SAME TIME

Viola riviniana

FIGURE 12

SURVIVORSHIP curves of seedlings and vegetative shoots 'born' at the same time - Viola riviniana

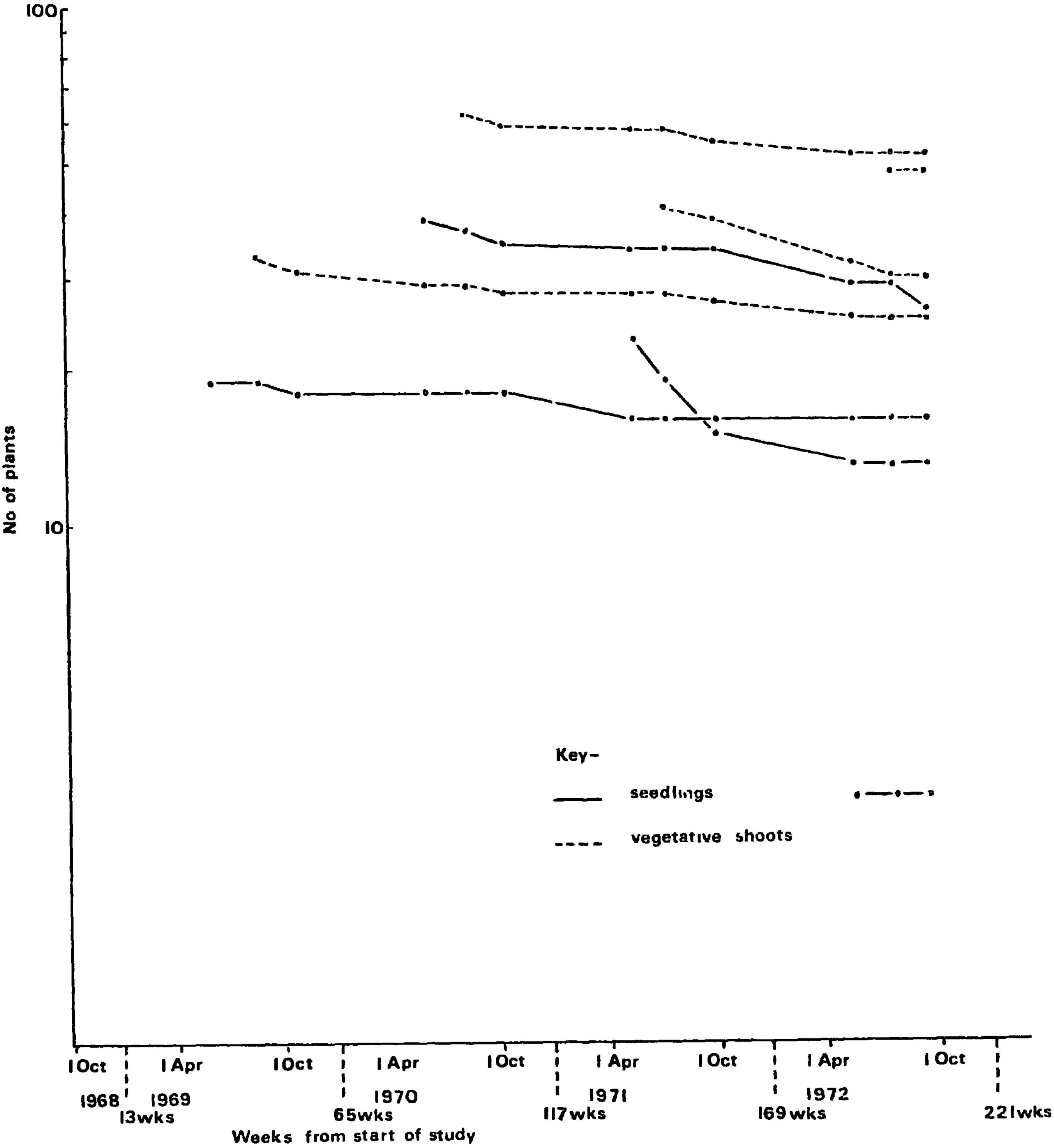


Figure 13

BEHAVIOUR OF INDIVIDUALS IN QUADRAT 8B.2

Viola riviniana

FIGURE 13 Behaviour of individuals in quadrat 8B·2 - *Viola riviniana*

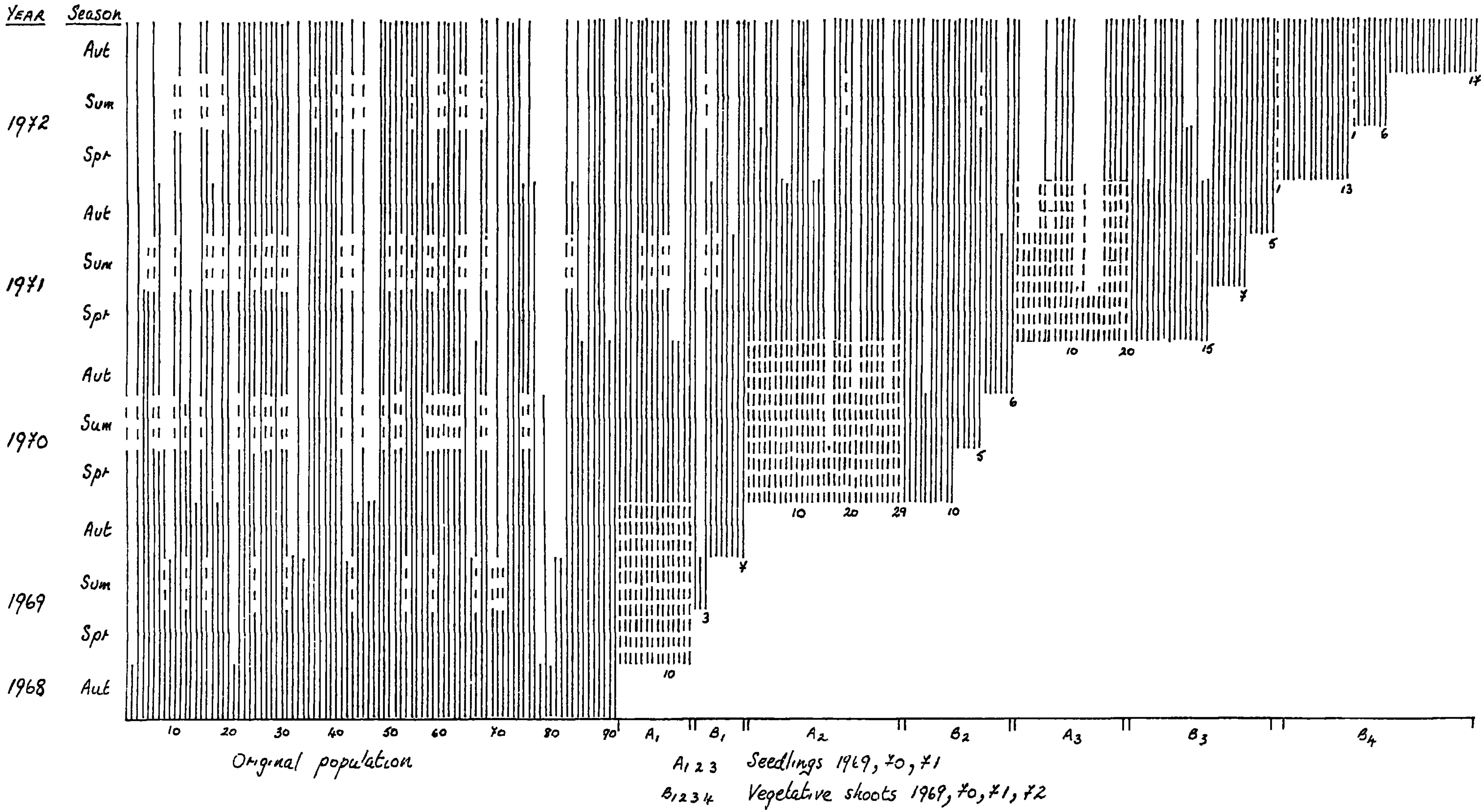


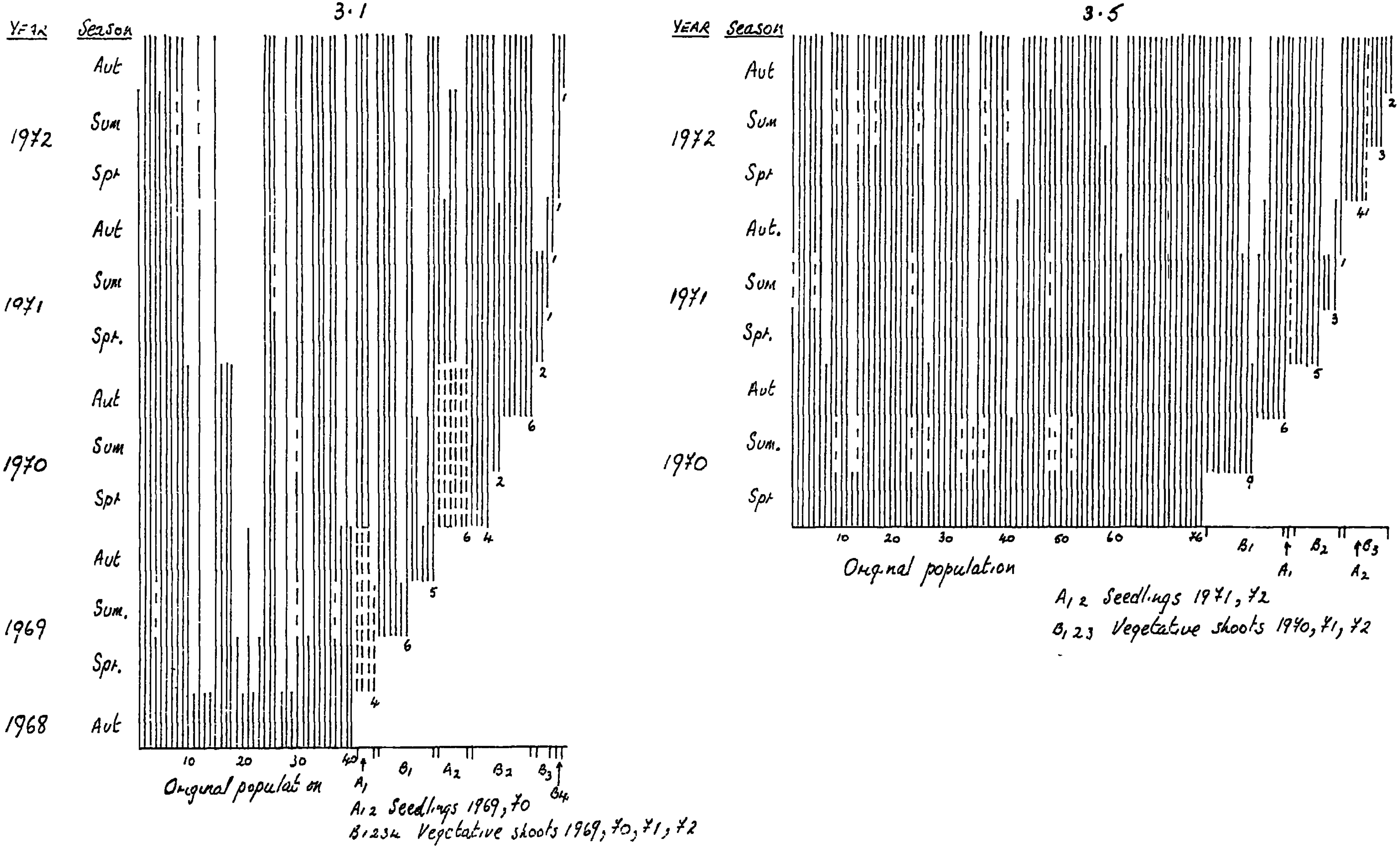
Figure 14

BEHAVIOUR OF INDIVIDUALS IN

QUADRATS 3.1 AND 3.5

Viola riviniana

FIGURE 14 Behaviour of individuals in quadrats 3·1 and 3·5 - <u>Viola riviniana</u>



CHAPTER SIX

VIOLA RUPESTRIS X RIVINIANA

SECTION 1: INTRODUCTION

This hybrid of Viola rupestris and Viola riviniana is a small rosulate plant similar in form to the Viola rupestris parent. The hybrid flowers prolifically but the flowers are sterile and reproduction is by means of new rosettes produced from soboles (root shoots), a character inherited from the Teesdale Viola riviniana parent. For the purpose of this study the individual or 'unit of reproduction', is considered to be any rosette arising from a root shoot.

Over the study period no seedlings, which had arisen from the germination of seed set following cross pollination between the two parents, were observed. On Widdybank Fell the hybrid is very restricted in its distribution indicating that cross pollination and seed set only occurs very infrequently. In view of the small number of ripe fruits which were recorded from open flowers of each ~~both~~ parents (Chapters four and five) this is perhaps not surprising. As far as is known, no similar hybrids have been found at the other two British stations where the parents occur together, and there are no reports in the literature of its occurrence anywhere else in Europe

The large size of the clones, some several metres across, indicates that once a plant has become established its vegetative mode of reproduction enables very dense populations of plants to be built up. Single plants and small groups of two or three individual plants were observed on the Fell but it is not known whether they lack the ability to produce soboles or were very recently established individuals.

Within the clones where permanent quadrats had been established individual rosettes were long-lived and population turnover and recruitment rates were low. Thus the life strategy of this species was very similar to the two parents, although there was no recruitment from seedlings.

SECTION 2: PERMANENT QUADRATS

Two sites (3 and 9) were selected for this hybrid on Widdybank Fell, both in heavily grazed sugar limestone turf. In each of the quadrats established at these two sites the individual rosettes were growing very close together and it is possible that the plants in each of the quadrats were part of clones.

Quadrat 3.3 was situated on a south west facing slope just above the reservoir's top-water line. The completely closed vegetation was dominated by Festuca ovina and Sesleria caerulea with Helianthemum chamaecistus, Thymus drucei, Briza media, Plantago maritima, Lotus corniculatus and Carex flacca also present.

Quadrat 9.1 was situated in the same area where Viola rupestris was recorded, at more than 500 metres from the reservoir. Here the vegetation was more open with some bare ground and moss cover. The vegetation was dominated by Sesleria caerulea and Festuca ovina with Viola rupestris x riviniana very frequent. Carex flacca, Potentilla erecta, Viola tricolour, Polygonum viviparum, Selaginella selaginoides, Koeleria gracilis and Thymus drucei were also present in the quadrat.

Each of the permanent quadrats had a sample site associated with it.

SECTION 3: POPULATION FLUX

A gradual increase in the number of individuals in the two quadrats was observed over the period of recording (Figure 15). These increases, expressed as a percentage of the originally recorded mixed-age population for the quadrats 3.3 and 9.1, were 38 and 20 respectively. The change in the total population was very gradual with no seasonal influences apparent such as were shown in the curves for Viola rupestris (Figure 4).

There is an indication in the curves that increases in 1969 and 1970 were followed by a levelling-off in 1971 and a slight decrease in numbers in 1972. The season of 1970, which for Viola rupestris and Gentiana verna was favourable to vegetative reproduction, also showed an increase in numbers of the hybrid which was related to a greater number of shoots appearing and becoming established in that year. The total population in quadrat 3.3 showed a similar increase in 1971.

The survival curves for the originally recorded mixed-age population are very shallow indicating that within each quadrat the rate of loss of individuals was very slow (Figure 16). Half-life values based on the decay in the number of individuals in the original mixed-age population over the period of recording indicate that the time taken for complete replacement of the population may take up to 34 years.

The estimated half-life values for the individuals in quadrats 3.3 and 9.1 were 17 and 10 years respectively.

The linear nature of these curves as well as those for the individuals of known age shown in Figure 17 indicates that the rate of decay has been constant. All the curves correspond to Deevey (1947) type 2. As with the two other violet species these curves show that the risk of mortality for all individuals of the hybrid was not affected by the age of the rosette.

The very steady slow rate of decay within the population coupled with the correspondingly low rate of recruitment resulted in a stable population being maintained over the study period.

SECTION 4: SEASONAL SURVIVAL AND ANNUAL RECRUITMENT

Seasonal survival over approximately six-monthly periods showed some variation between the two quadrats and between the seasons (Table a). The individual values represent the proportion of plants surviving over each period as a rate per individual present at the beginning of each time interval. For this plant the number 'at risk' includes all surviving vegetative shoots regardless of their age; as the hybrid is sterile there are no seedlings. Data are not available for the season Spring 1969 to Spring 1970 for quadrat 3.3 as it was not established until Spring 1970.

Variation between individual survival rates is not large but the three lowest between-season figures are statistically significantly different at the 5% level of probability from the values for Winter 1970/71 and Winter 1971/72. This result suggests that as with

Table a

SEASONAL SURVIVAL

Viola rupestris x riviniana

	QUADRAT		
SEASON	3.3	9.1	
Summer 1969	No record	0.90	0.90 ± 0.02
Winter 1969/70	No record	0.89	0.89 ± 0.03
Summer 1970	0.97	0.92	0.94 ± 0.01
Winter 1970/71	0.98	0.94	0.95 ± 0.01
Summer 1971	0.98	0.91	0.94 ± 0.01
Winter 1971/72	0.96	0.95	0.96 ± 0.01
Summer 1972	0.93	0.90	0.91 ± 0.01
	0.96 ± 0.01	0.92 ± 0.01	

Overall seasonal survival for each quadrat population both between the quadrats and between the seasons is shown ± standard error

Viola rupestris the risk of mortality is greater during the growing season. It is possible that adverse climatic conditions over the period Autumn 1968 to Autumn 1970, coupled with the greater stresses imposed on the plants when they were growing and flowering, resulted in the reduction in survival rates which can be seen for these seasons in the table. The higher survival rates for the Winters 1970/71 and 1971/72 suggest that during these seasons the mild Winters may have imposed less stress on individuals, particularly at a time when they were dormant.

Recruitment in the hybrid was entirely by new vegetative shoots. The annual rate of recruitment of these new plants to the quadrat populations is shown in Table b, where the figures are expressed as a rate per individual present in each quadrat in the Summer of each year. The values differ considerably for each season and it is clear that in 1970 for quadrat 9.1, at least, there was a large influx of new plants compared with the other years. However, recruitment of new plants into quadrat 3.3 was relatively low throughout, with 1971 having the highest recruitment rate.

SECTION 5: AGE-SPECIFIC SURVIVAL AND AGE-DISTRIBUTION

Survival of vegetative shoots of known age in the two quadrats was independent of the age of the individuals. The curves, which show the decay in the number of new shoots (summed for each season), are ~~very~~ linear and differ only slightly from each other. They conform closely with Deevey (1947) type 2, and as for the two parent species, they indicate that the risk of mortality was constant irrespective of the age of the individuals.

Table b

RATE OF ANNUAL RECRUITMENT OF NEW VEGETATIVE ROSETTES

Viola rupestris x riviniana

	QUADRAT	
YEAR	3.3	9.1
1969	No record	0.12
1970	0.15	0.37
1971	0.20	0.17
1972	0.14	0.08

As with the survival curves for the originally recorded mixed-age populations the slopes are very shallow and between some recordings show no loss of individuals at all. Thus the slow rate of turnover, indicated by the half-life values based on the decay of the original populations, is shown also by the survival curves for individuals of known age.

The distribution of the different age classes present in the quadrats at the end of the study period in Autumn 1972 show that there was a very high proportion of mature individuals in the population, (Table c). In both quadrats approximately 50% of the total population was made up of plants which were present at the time when the first recording was carried out. The large number of individuals in quadrat 9.1 surviving from the year Autumn 1969 to Autumn 1970 reflect the high recruitment rate in that quadrat in the Summer of 1970.

Plants were able to flower in their second year and if this is taken as an indication of maturity, then they can make a contribution to the replacement of the population by the production of soboles when they are two years old. However, only a few plants actually flowered in their second year and Viola rupestris x riviniana, as with its parents, appears to be a species which takes several years to mature, has a low rate of mortality and a correspondingly low recruitment rate.

SECTION 6: REPRODUCTIVE PERFORMANCE

Reproductive performance can only be discussed for this plant in terms of the number of flowers produced as both the open and closed flowers are sterile. The number of plants flowering, that is, Table c

DISTRIBUTION OF AGE CLASSES IN EACH QUADRAT
AT THE END OF THE STUDY PERIOD

Viola rupestris x riviniana

		QUADRAT	
	AGE IN YEARS	3.3	9.1
Present Spring 1969	> 3½	No record	82
'Born' year Spr. 1969-Aut. 1969	3-3½	96*	13
'Born' year Aut. 1969-Aut. 1970	2-3	14	42
'Born' year Aut. 1970-Aut. 1971	1-2	31	26
'Born' year Aut. 1971-Aut. 1972	< 1	23	13

* Individuals > 2½ years old, first recorded Spring 1970

producing either open or closed flowers, was consistently greater at site 9, where data from quadrat 9.1 and sample site 9ss1 are included. There was little difference in the number of plants producing flowers between the years for both site 9 and site 3. Data for site 3 was obtained from quadrat 3.3 and sample site 3ss2, (Table d).

The differences between the number of open and closed flowers produced at each site was quite marked and unlike Viola rupestris and Viola riviniana quite large numbers of open flowers were produced at both sites compared with the number of closed flowers. In 1970 more open flowers were recorded than closed and a similar result was obtained at site 3 in 1972. (The number of closed flowers was probably underestimated in 1970 as some were not properly identified as such). The lowest number of open flowers was recorded in 1971 when there were more closed flowers than open flowers.

SECTION 7: SPECIES BIOLOGY

The hybrid of Viola rupestris and Viola riviniana is similar in form to the Viola rupestris parent but with leaves shaped like the Viola riviniana parent. The plant reproduces by means of new rosettes produced from soboles, a character inherited from the Viola riviniana parent. The hybrid is perennial and individual rosettes die down during the Winter period.

Individual plants are long-lived, as can be seen by the survivorship curves (Figures 16 and 17) and the half-life values of 17 and 10 years, which indicate that some plants may live for as long as 34 years or more.

Table d

PRODUCTION OF FLOWERS

Viola rupestris x riviniana

YEAR	SITE	Total No. Plants	No. flowering	No. of flowers	
				Open	Closed
1969	3	39	4	No record	
	9	623	32	No record	
1970	3	356	35	13	0
	9	308	47	13	1
1971	3	346	38	3	12
	9	344	58	1	47
1972	3	382	30	13	8
	9	328	57	15	38

There were no obvious signs of loss of individual rosettes by grazing or pulling out by sheep. Longevity was not affected by the plant flowering; indeed many plants flowered in two, three and, for one plant, four successive years (Figures 18 and 19). These figures show the behaviour of the quadrat population 3.3 and 9.1 respectively, where each line represents an individual, and flowering is shown by a broken and dotted line, after Tamm (1948).

No seed is set as the hybrid produces flowers which are sterile. These flowers may be of two kinds, as in the parents' species, chasogamous (open) and cleistogamous (closed). The period of production of flowers was very similar to that for Viola rupestris with open flowers appearing in May on Widdybank Fell. Closed flowers started to appear in May also but whereas open flowers were only produced over a period of 3 to 4 weeks, closed flowers appeared throughout the growing season.

The mean number of flowers per flowering plant is shown in Table e, and it can be seen from the figures that the mean number of open flowers was quite high. In two of the three years the number of open flowers was greater than the number of closed, in 1970 for both sites and in 1972 for site 3 only. In all three of the years the number of open flowers produced was greatest at site 3 whilst the number of closed flowers were greater at site 9. These results suggest that at the two sites there were factors which affected the ability of plants to produce the two kinds of flowers, in different ways.

Table e

FLOWER PRODUCTION

(MEAN FLOWERS PER FLOWERING PLANT)

Viola rupestris x riviniana

YEAR	SITE	Open flowers	Closed flowers
1970	3	0.37 ± 0.13	0.00
	9	0.29 ± 0.06	0.02 ± 0.02
1971	3	0.21 ± 0.06	0.32 ± 0.08
	9	0.02 ± 0.02	0.81 ± 0.12
1972	3	0.43 ± 0.13	0.27 ± 0.09
	9	0.26 ± 0.06	0.67 ± 0.13

Figures for flower production are given as a mean per flowering plant ± standard error

SECTION 8: LIFE STRATEGY

The small plant depends entirely on vegetative reproduction for propagation. Longevity of individuals is high and the rate of turnover of the population correspondingly slow. Half-life values indicate that it may take as long as 34 years for complete replacement of the population.

The relatively slow rate of turnover requires only a low rate of recruitment to replace lost individuals. The study reveals that recruitment was greater than mortality, and as a result of the high survival rate of the new shoots the total number of individuals in each quadrat increased. Thus during the study period, at least, the population increased in density.

No other hybrids of this kind have been found at the two other localities in Britain, where the parents occur together. This fact combined with the very restricted distribution of the plants in Teesdale suggests that cross pollination and successful establishment of seedlings only occurs infrequently. Some of the colonies are quite large and may have been derived from a single seedling. On Widdybank Fell there are also several small colonies which may be small because they are recent in origin or because the plants did not inherit the ability to produce soboles.

Once a plant is established it is clear from the present study that it is able to reproduce very successfully. The apparent absence of this hybrid from Europe as a whole suggests that the factors controlling the existence of this hybrid act directly through the prevention of cross-pollination. Since open flowers are only produced in fairly small numbers in both parents and very few ripe fruits are formed from these flowers it is not surprising that the hybrid is so restricted.

Figure 15

TOTAL POPULATIONS

Viola rupestris x riviniana

FIGURE 15

TOTAL POPULATION–*Viola rupestris x riviniana*

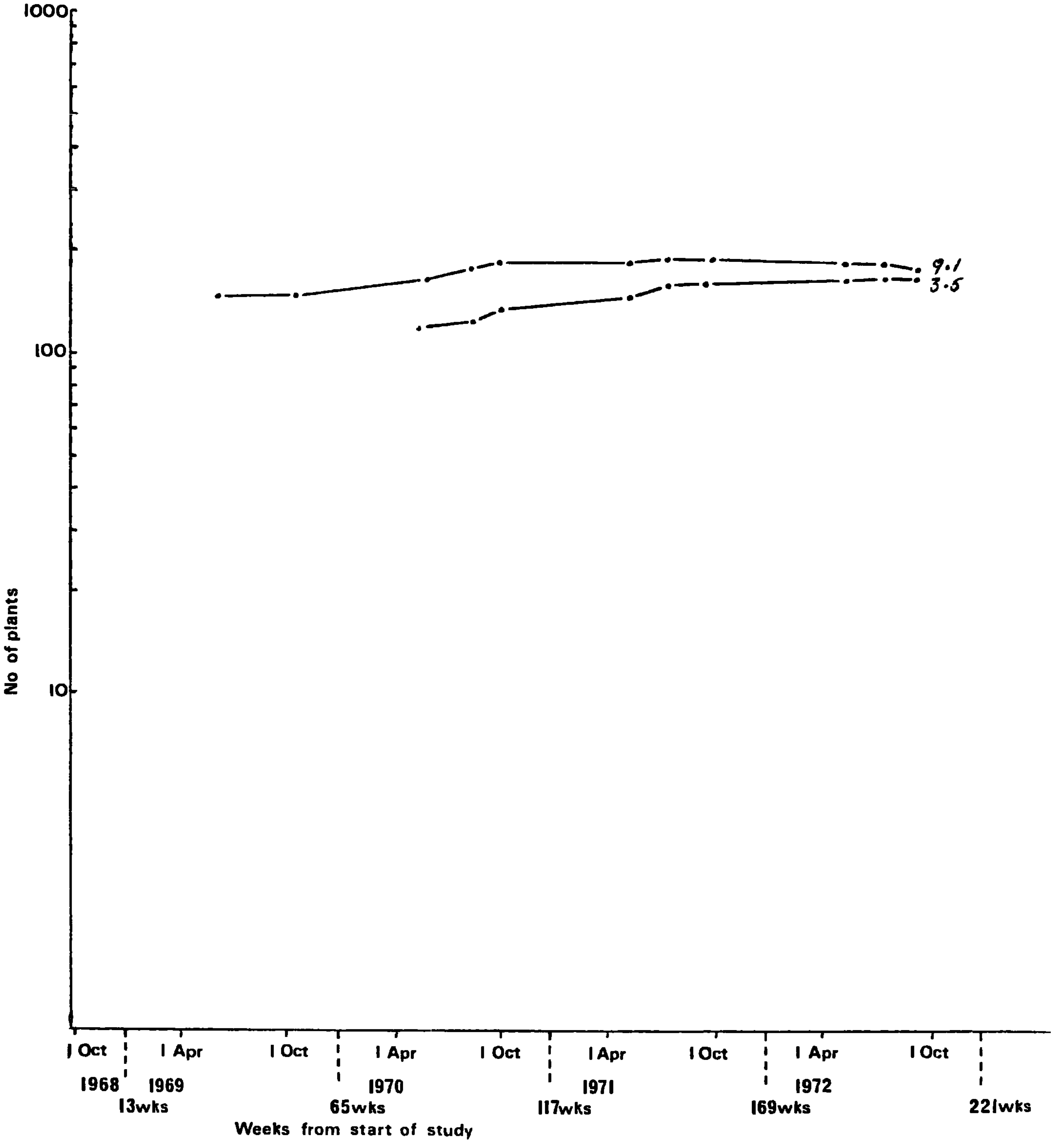


Figure 16

SURVIVORSHIP CURVES OF MIXED-AGE POPULATIONS

Viola rupestris x riviniana

FIGURE 16

SURVIVORSHIP curves of mixed age populations – *Viola rupestris x riviniana*

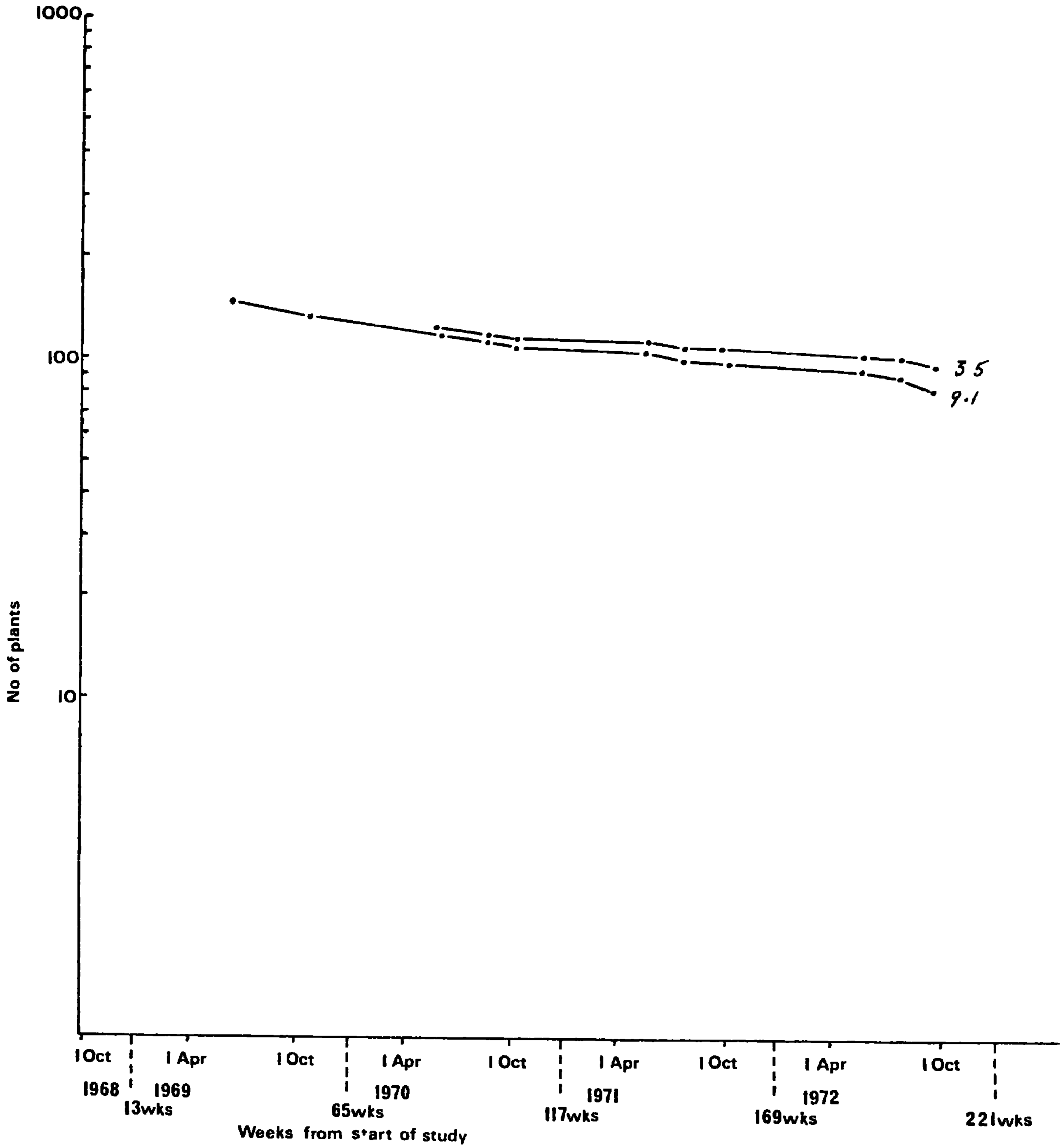


Figure 17

SURVIVORSHIP CURVES OF VEGETATIVE
SHOOTS 'BORN' AT THE SAME TIME

Viola rupestris x riviniana

FIGURE 17

SURVIVORSHIP curves of vegetative shoots 'born' at the same time – *Viola rupestris x riviniana*

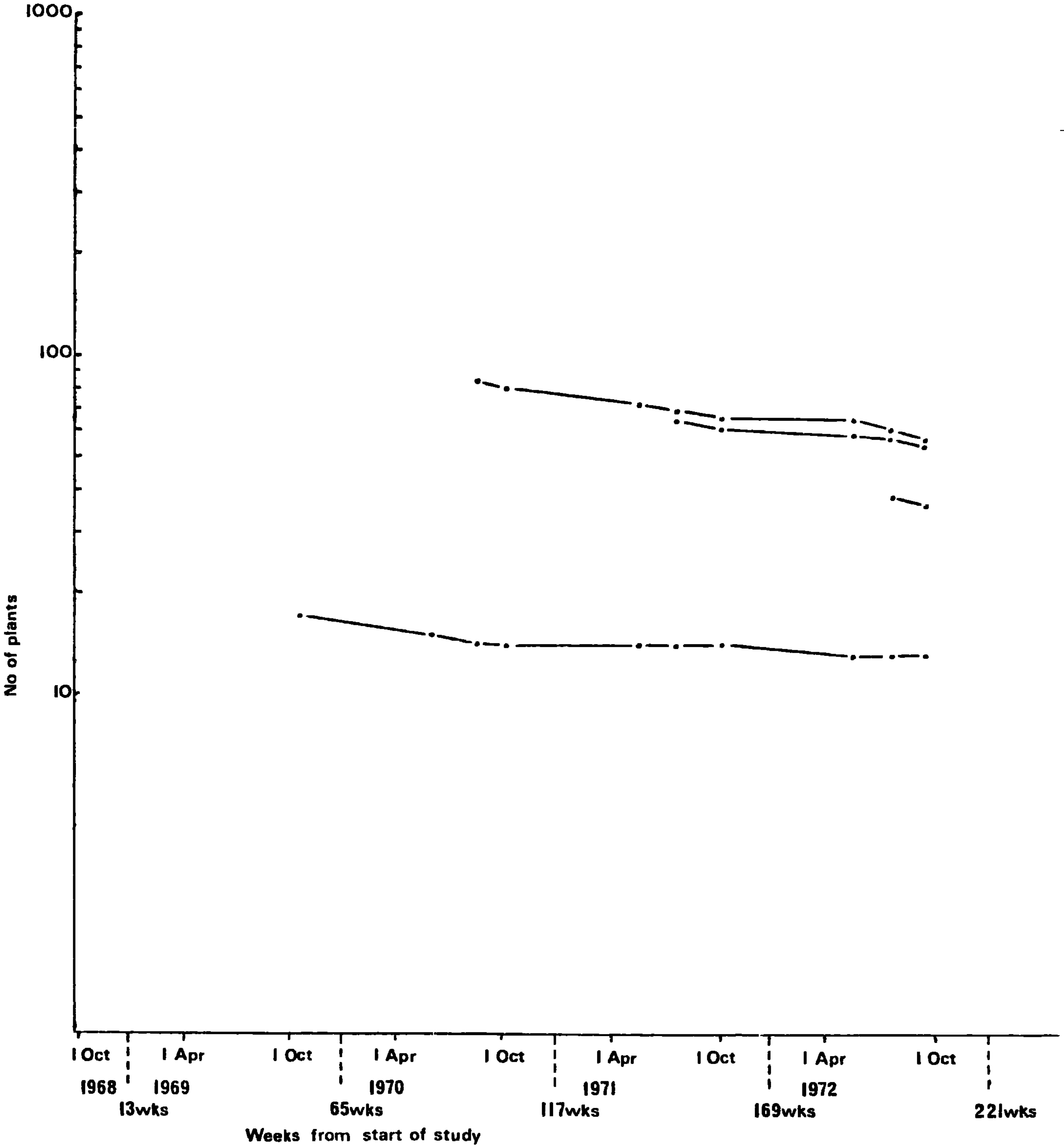


Figure 18

BEHAVIOUR OF INDIVIDUALS IN QUADRAT 3.3

Viola rupestris x riviniana

FIGURE 18 Behaviour of individuals in quadrat 3·3 - Viola rupestris × riviniana

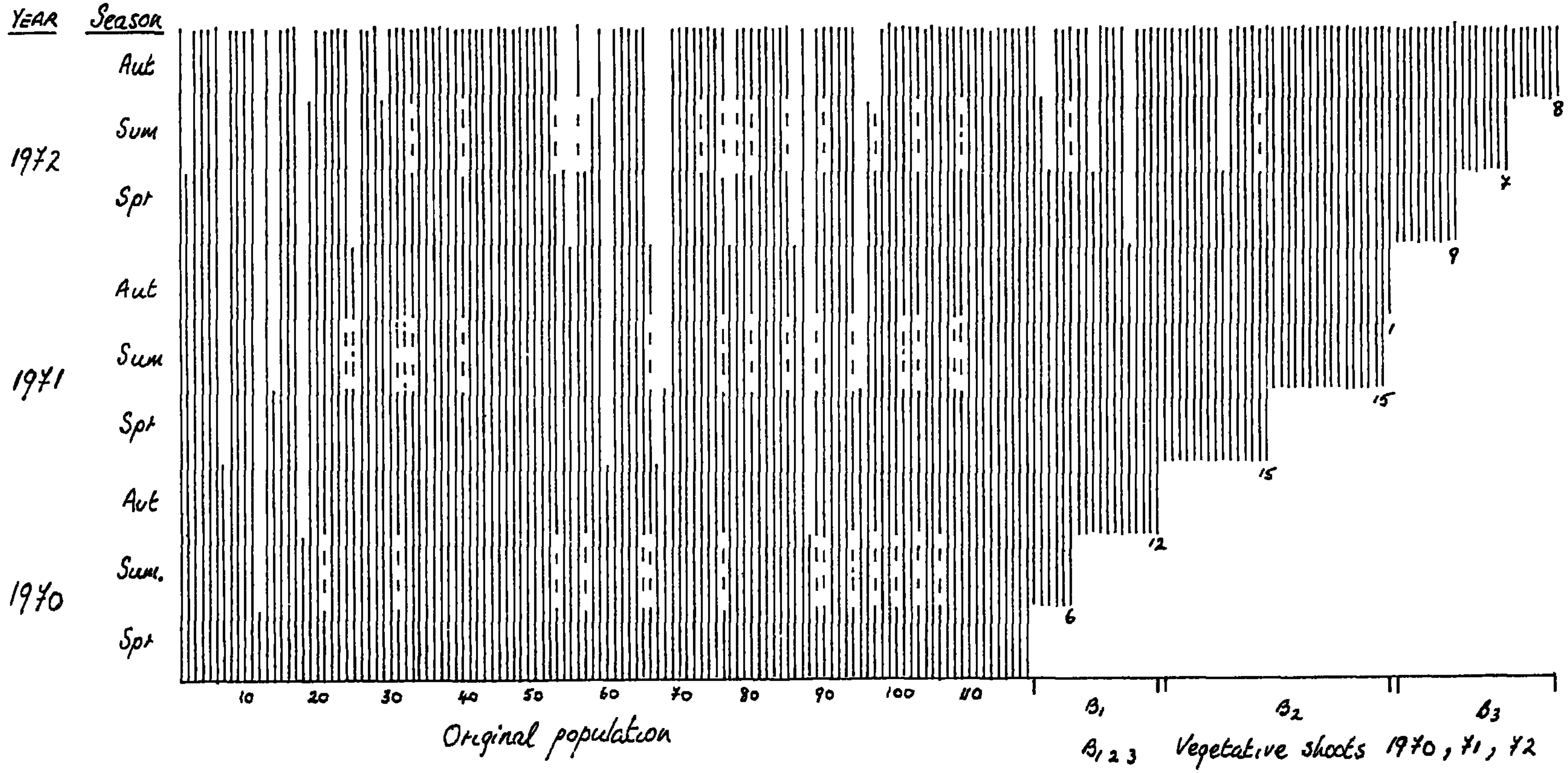
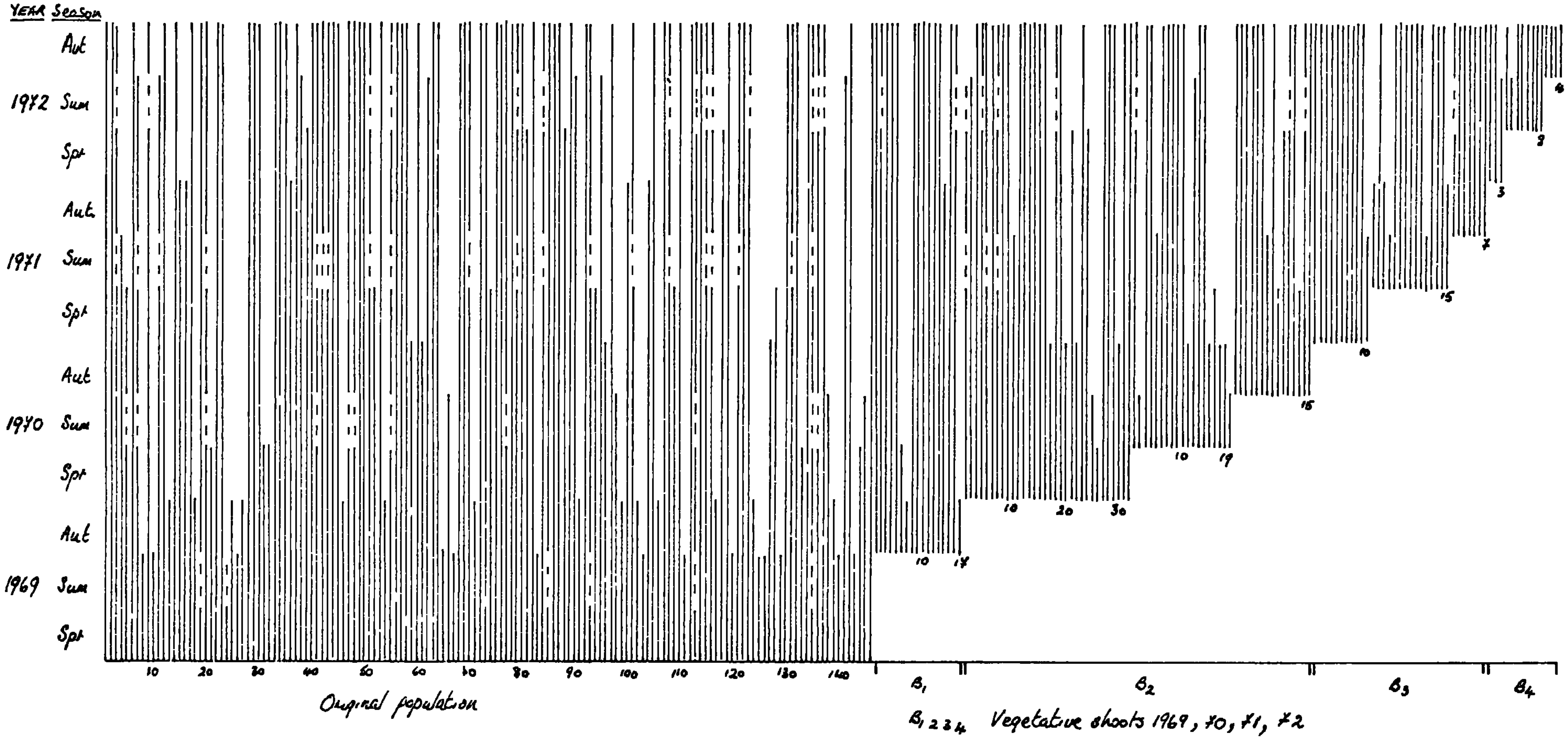


Figure 19

BEHAVIOUR OF INDIVIDUALS IN QUADRAT 9.1

Viola rupestris x riviniana

FIGURE 19 Behaviour of individuals in quadrat 9·1 - Viola rupestris x riviniana



CHAPTER SEVEN

POLYGALA AMARELLA

SECTION 1: INTRODUCTION

Polygala amarella (Polygala amara), Fearn (1971) is characterised by having a basal rosette of leaves. Young plants have a short, simple main stem but mature plants may produce lateral branches, which also have a rosette of leaves at their base, either after flowering or because of grazing. (In Figures 24 and 25 this branching is shown by a branch on the line representing an individual plant).

The individual or 'unit of reproduction' in this species is considered to be any plant which arises from a seed. Although branches are produced these remain attached to the main stem and unlike Viola rupestris, where new rosettes arise from underground stems and form recognisable units, they clearly form part of the original rosette.

Individual plants are short-lived often flowering in successive years before dying. Recruitment during the study period was entirely by germination of seed and subsequent establishment of seedlings. Germination occurred mainly during the Summer months of July and August and was very variable (Section 7).

Plants were often observed partially eaten by sheep, particularly when they were flowering, but this only occasionally resulted in the prevention of the production of seed. Flowering and seed production occurred over an extended period in the Summer months, and in some plants loss of the flowering stem at the end of May to the beginning of June resulted in branching and the production of flowers later in the season. At least one individual which was grazed during this period went on to produce 104 seeds on 15 branches in one of the sample sites later in the same season.

Plants in Upper Teesdale are restricted to a limited number of small colonies of a few hundred individuals each. These individuals are much less vigorous than those occurring at another location in Yorkshire, where plants were not only bigger and their flowering apparently more prolific, but they were also more widely distributed. This observation suggests that the extreme climatic conditions experienced in Upper Teesdale restrict the growth and ability of plants to flower.

In Upper Teesdale there are two genetically different plants. The normal blue-flowered variety occurs mainly on Widdybank Fell in several small colonies and in one small colony on Cronkley Fell. A pink-flowered plant grows in two small but dense colonies, only on Cronkley Fell.

SECTION 2: PERMANENT QUADRATS

Five permanent quadrats were established, four on Widdybank Fell at sites 6 and 7, which were 200 to 250 metres from the top-water line of the reservoir, and one on Cronkley Fell. The quadrats on Widdybank Fell were situated in heavily grazed sugar limestone turf close to or amongst Calluna vulgaris. The quadrat on Cronkley Fell was recorded for the pink-flowered variety of Polygala amarella. The vegetation contained Calluna vulgaris and Empetrum nigrum and was very closely grazed by both rabbits and sheep unlike the quadrats on Widdybank Fell which were grazed exclusively by sheep. Details of the vegetation in the individual quadrats are given below.

Quadrat 6.1 was dominated by Sesleria caerulea and Festuca ovina but with some moss/lichen cover. Details of the other species present are given in Chapter five, Section 2, as this quadrat was also recorded for Viola riviniana.

Quadrat 7.1 was situated in an area of sugar limestone turf grading into Calluna vulgaris. The vegetation was dominated by Sesleria caerulea and Festuca ovina with Kobresia simpliciuscula, Thymus drucei, Campanula rotundifolia, Gentiana verna, Antennaria dioica, Briza media, Plantago maritima also present together with some moss/lichen cover. A map showing the type of vegetation in one metre length of this quadrat is shown in Figure 20.

Quadrat 7.2 was almost completely dominated by Sesleria caerulea with little bare ground or moss/lichen cover. The vegetation in this quadrat, which was close to quadrat 7.1, differed in that Calluna vulgaris and Kobresia simpliciuscula were both absent. This quadrat was also recorded for Gentiana verna (Chapter nine)

Quadrat 7.3 was atypical in that Polygala amarella was growing in a moss/lichen substrate overlying bare rock. A relatively large proportion of the area was without any vegetation cover and part contained Calluna vulgaris. This quadrat was also recorded for Draba incana (Chapter eight).

Quadrat 10.2 was situated on Cronkley Fell close to a colony of rabbits and consequently the turf was quite closely cropped. The vegetation was dominated for the most part by Sesleria caerulea and

Figure 20

MAP OF VEGETATION IN QUADRAT 7.1

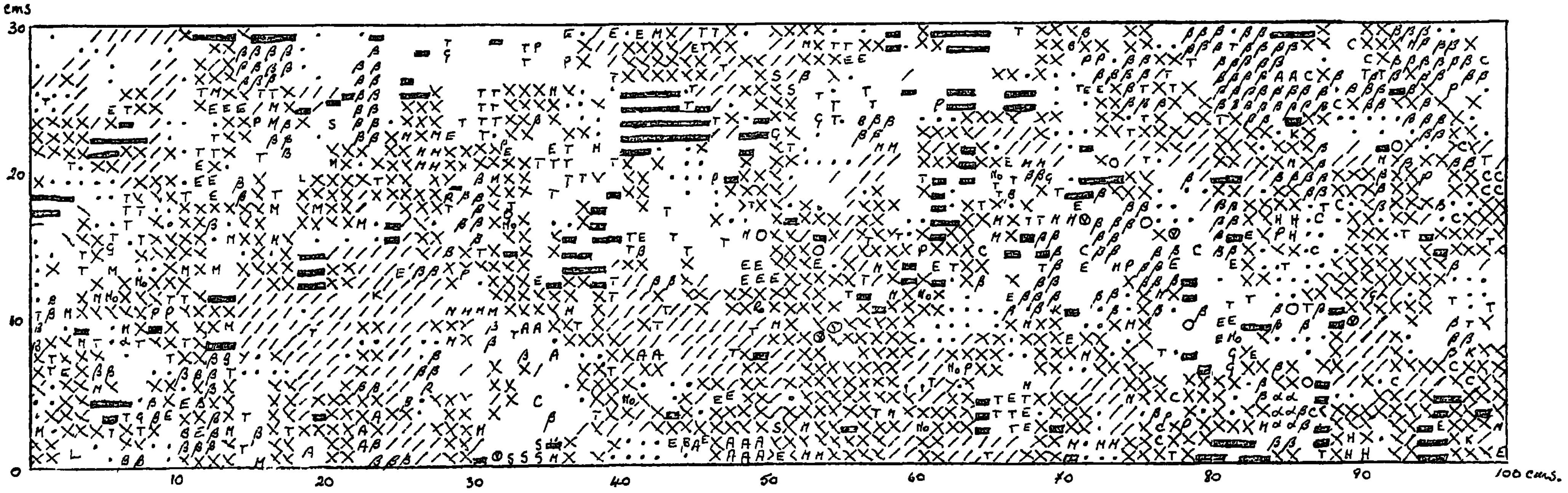
Polygala amarella

FIGURE 20 Map of Vegetation in quadrat 7·1 - *Polygala amarella* (June 1970)

KEY to main species: · *Sesleria caerulea*, / *Festuca ovina*, ▬ *Kobresia simpliciuscula*,

M *Briza media*, A *Minuartia verna*, T *Thymus drucei*,

β lichen, S *Plantago maritima*, H *Prunella vulgaris*.



Festuca ovina although Calluna vulgaris and Empetrum nigrum covered part of the quadrat. The pink-flowered plants were able to survive and flower in the denser stand of Empetrum nigrum.

Because of the very restricted population of Polygala amarella on both Fells, two sample sites only were established on Widdybank Fell close to quadrats 7.1 and 7.2. One sample site was recorded in association with quadrat 10.2 on Cronkley Fell and contained pink-flowered plants.

SECTION 3: POPULATION FLUX

Change in the total population of individual plants in each quadrat was irregular and often large (Figure 21). The total number includes all the surviving plants present at the time of recording except seedlings which had not survived the Winter period. The increase in the total population which is apparent in the Springs of 1969 and 1970 is due to the inclusion of seedlings germinating in the previous year and surviving to the Spring.

The very large seed germination of 1969 and the subsequent survival of the seedlings is reflected by the rise shown in the curves in Spring 1970, a rise which can be seen for the individuals in all the quadrats. Following this steep rise the curve for the total population in quadrat 6.1 shows that there was a slight decline in numbers followed by another rise in the Spring of 1971. This was repeated in 1972 such that overall there was an increase of 110% in the total population over the period of recording.

The curves for the total populations in quadrats 7.1 and 7.2 show an increase in numbers in 1971 followed by a slow decline over the Winter 1971/72 and Summer 1972 such that the total population in each quadrat in Autumn 1972 was slightly lower than that recorded in Autumn 1968. In the case of quadrats 7.3 and 10.2 the increase in the total population in 1970 was followed by a steady decline over the rest of the study period. In the former of these quadrats there was an overall increase of 171% between Summer 1969 and Autumn 1972, in the latter a drop of 21% between Autumn 1968 and Autumn 1972.

These results show that survival of the population of Polygala amarella on Widdybank and Cronkley Fells depends on the ability of the species to produce seed, which in favourable years germinates well. Without the very large seedling recruitment in 1969 most quadrats would have experienced a sharp fall in the number of individuals over the study period. The rate of germination (recruitment) in any year depends on the amount of seed produced in the previous year. (The occurrence of seedlings close to fruiting plants of the previous year suggests that germination occurred in the year following seed-set). Climatic factors affecting the actual germination of seed may also play an important role particularly if viable seed is stored in the soil or on the soil surface.

Survivorship curves for the originally recorded mixed-age population are steep, indicating that the rate of loss of individuals from the quadrats was high. On the whole the curves show a relatively steady decline in numbers, although in three of the quadrats there were a large number of deaths in some seasons. Quadrats 6.1 and 7.1 showed a steep decline in numbers between the Spring and Summer records in 1969; quadrat 7.1 showed a further relatively high rate of mortality between the Summer and Autumn records of 1970 and 1972. Quadrat 7.3 also showed a sharp increase in the rate of mortality between the Summer and Autumn records of 1971, although in this case the loss was of only 2 plants from the 5 surviving from Summer 1969, (Figure 22).

Half-life values based on the decline in the number in the original population over the period of recording show that a few individual rosettes may live for up to 14 years (Table a). However, the highest value was obtained for the individuals in quadrat 7.3 where only 7 individuals were recorded when the quadrat was set up, 3 of which survived to Autumn 1972. Clearly with half-life values as low as 2.7 years, this figure of 14 years is probably a maximum possible life-span and a more realistic estimate of longevity is 6 to 10 years.

SECTION 4: SEASONAL SURVIVAL AND ANNUAL RECRUITMENT

The seasonal survival over approximately six-monthly periods varied a great deal between the quadrats and between years (Table b). Values range from 0.54 for the individuals in quadrat 6.1 over the Summer 1969 to 0.99 for the same quadrat in Summer 1971. The individual values represent the proportion of plants surviving over each season, expressed as a rate per individual present at the beginning of each time interval. For this species the number 'at risk' includes all surviving plants, but only including seedlings after they had survived one Winter period.

Table a

HALF-LIFE VALUES

Polygala amarella

Quadrat	Half-life (years)	No.
6.1	6.4	38
7.1	2.7	31
7.2	4.3	49
7.3	6.6	7
10.2	3.6	96

No. - Number of individuals in the originally recorded mixed-age population

Table b

SEASONAL SURVIVAL

Polygala amarella

QUADRAT

SEASON	6.1	7.1	7.2	7.3	10.2	
Winter 1968/69	0.92	0.94	0.82	No record	0.76	0.83 ± 0.03
Summer 1969	0.54	0.66	0.73	No record	0.75	0.69 ± 0.04
Winter 1969/70	0.79	0.89	0.79	0.71	0.71	0.77 ± 0.04
Summer 1970	0.93	0.82	0.89	0.71	0.89	0.86 ± 0.02
Winter 1970/71	0.92	0.89	0.86	0.93	0.84	0.88 ± 0.02
Summer 1971	0.99	0.94	0.79	0.91	0.92	0.91 ± 0.02
Winter 1971/72	0.93	0.82	0.75	0.81	0.74	0.80 ± 0.02
Summer 1972	0.94	0.72	0.89	0.68	0.85	0.86 ± 0.02
	0.90 ± 0.01	0.84 ± 0.02	0.82 ± 0.02	0.80 ± 0.03	0.82 ± 0.01	

Overall seasonal survival for each quadrat population both between quadrat and between season is shown ± standard error

The lowest between season survival rate was recorded for the Summer season 1969, and this figure is statistically significantly different at the 5% level of probability than all the other values. The Winter 1969/70 figure is also significantly lower than all but the seasons Winter 1968/69 and Winter 1971/72. The seasonal value for Winter 1971/72 is statistically significantly lower at the 5% level of probability than the Winter 1968/69, Summer 1970, Winter 1970/71, Summer 1971 and Summer 1972 figures. It can be seen from these comparisons that there is no indication that mortality was consistently greater during either the Winter or Summer seasons. The variation between the seasons was, in fact, inconsistent and often large.

The differences when comparisons are made between quadrats are less marked, with overall survival rate for the individuals in quadrat 6.1 being statistically greater at the 5% level of probability than the other quadrat values. None of these other values come near to being significantly different from one another. The reason for the higher rate of survival of the individuals in quadrat 6.1 is difficult to understand, as there were no obvious differences in the vegetation or grazing pressure which might explain it.

Recruitment in Polygala amarella was entirely by the production of seed, its germination and subsequent establishment of seedlings. Seed germination occurred throughout the growing season following the year of seed production, and was concentrated mainly during the mid-Summer months of July and August. The figures given in Table c show

Table c

RATE OF ANNUAL SEEDLING RECRUITMENT

<u>Polygala amarella</u>

QUADRAT

YEAR	6.1	7.1	7.2	7.3	10.2	
1969	2.53	1.37	2.10	6.43	1.97	2.22*
1970	0.43	0.78	0.59	0.30	0.22	0.40*
1971	0.40	0.04	0.15	0.12	0.13	0.17*
1972	0.19	0.38	0.49	0.32	0.19	0.27*
	0.51*	0.50*	0.67*	0.69*	0.47*	

Figures shown with an asterisk represent the annual seedling recruitment rates for the summed totals for each quadrat and year the number of seedlings which appeared in each year expressed as a rate per individual present in the quadrats at the Summer recording.

The recruitment rates shown in the table vary considerably between years but very little between the quadrats. Figures range from 6.43 in 1969 in quadrat 7.3 to 0.04 in quadrat 7.1 in 1971, but consistently the highest values occurred in 1969. Since seed germination appears to take place in the year following seed-set (Section 7) the very high recruitment of seedlings in 1969 may have been related to the production of seed in the previous year. No results are available for reproductive performance in 1968 and, therefore, it is not possible to determine whether seed production in that year was high enough to have resulted in the recruitment rate observed in 1969 of 2.22 seedlings per individual present in the population. However, it is clear that either a season favourable to flowering and seed-set in 1968, or a season favourable to seed germination in the following year, or both, resulted in a seedling recruitment rate in 1969 which was five times greater than in the other years.

Conversely there is no indication that low seed production in 1969, 1970 and 1971 resulted in the relatively low rates of recruitment observed in 1970, 1971 and 1972. However, it is clear that with an annual mortality rate of 31 plants per 100 present in the population, recruitment in 1971 and 1972 of 17 and 27 per 100 plants was not high enough to ensure replacement of lost individuals in those years. Thus the very high recruitment in 1969 was necessary to ensure that the population of Polygala amarella did not decrease considerably over the period of recording. This result indicates that Polygala amarella must depend for its long-term survival on the occasional year being particularly favourable to seed production and/or germination.

SECTION 5: AGE-SPECIFIC SURVIVAL AND AGE-DISTRIBUTION

Survivorship curves for individuals of known age are linear and conform closely with Deevey (1947) type 2 (Figure 23). The linear nature of these curves indicates that there was a constant risk of mortality throughout the life of the individual, that is, that mortality in the species is age-independent. The data in the figure are represented by curves showing the decay in the total number of seedlings recorded in all the permanent quadrats in any one year, expressed as a Summer total and plotted on a logarithmic scale.

The seed was quite heavy and seedlings, upon germination, have large cotyledons which persisted at least through the first year of the plant's life. The absence of an increased mortality rate in the early stages of establishment particularly following germination, was probably due to the large seed size which provided an initial energy source enabling the seedling to overcome some of the rigours associated with this early phase in the plant's life.

The curves for each of the groups of seedlings recorded in the same year have very similar slopes indicating that not only was mortality independont of the age of the individual, but that the different cohorts had similar rates of decay. Thus the proportional representation of individuals of different ages in the population appears to be dependent on the initial number recruited and the time period over which the observations were made.

A large proportion of the individuals present in the quadrats in Autumn 1972 were individuals which appeared during the study period (Table d). Unlike the figures for the Violets, where large numbers of plants were more than 4 years old (that is, present at the beginning of the study), in Polygala amarella this age-group made up 20% or less of the total number of plants in the quadrats in Autumn 1972.

Clearly the large recruitment of seedlings in 1969 was extremely important to the maintenance of the population, since this age-group constituted a significant proportion of the quadrat populations in 1972. It is also important that plants begin to flower in relatively high numbers at this age and, therefore, are capable of making a contribution to the reproductive potential of the population. Although plants were able to flower when younger than this, they did so in smaller numbers (Section 7).

These figures confirm the conclusion indicated by the low half-life values, that individuals were short-lived. The relatively short life-span was coupled with early maturity (plants flowered in relatively high numbers when 3 and 4 years old; in Viola rupestris on the other hand, under natural conditions in Upper Teesdale, only one plant established from a seedling flowered during the study, when it was 4 years old).

SECTION 6: REPRODUCTIVE PERFORMANCE

Reproduction in Polygala amarella was entirely by means of the production of seed, its germination and the subsequent establishment of the seedlings. Plants were able to flower in their second year

Table d

DISTRIBUTION OF AGE-CLASSES IN EACH QUADRAT AT THE END OF THE STUDY PERIOD

Polygala amarella

		QUADRAT				
	AGE IN YEARS	6.1	7.1	7.2	7.3	10.2
Present Autumn 1968	> 4	14	3	11	3*	16
'Born' year Aut. 1968-Aut. 1969	3-4	28	10	14	10	37
'Born' year Aut. 1969-Aut. 1970	2-3	17	15	9	3	14
'Born' year Aut. 1970-Aut. 1971	1-2	21	1	5	3	9
'Born' year Aut. 1971-Aut. 1972	< 1	16	13	18	8	16

* Individuals > 3 years old, first recorded Summer 1969

although only one individual actually did so; more usually plants first flower in their third and fourth year (Figures 24 and 25 and Section 7).

Flowering began in mid-May and continued throughout the season until about mid-September, when fruits were often present. Flowers present at that time did not develop further. A maximum of two seeds can be produced in each capsule but often only one, and sometimes no ripe seed was present in apparently ripe capsules.

The number of plants present in the permanent quadrats and sample sites for each Fell is shown in Table e, together with the number of these which flowered. The figures for Widdybank Fell blue-flowered plants include data from quadrats 6.1, 7.1, 7.2 and 7.3 together with sample sites 7ss1 and 7ss2. The figures for Cronkley Fell pink-flowered plants include data from quadrat 10.2 and sample site 10ss2. The mean number of fruits per flowering plant and seeds per capsule used in estimating seed production per 100 plants are given in Section 7, Table f.

The potential for recruitment in this species is high when compared with the annual rate of loss of plants. Overall an annual mortality of 30 individuals per 100 in the quadrat populations could be compensated for ten times over in 1969 and 1970 on Widdybank Fell. However, it is clear from the recruitment figures (Table c) that only in 1969 did the number of seedlings approach the annual number of seeds which can be produced. In the other three years recruitment was very low compared with the number of seeds produced in the previous year.

Table e

ESTIMATED PRODUCTION OF SEEDS

<u>Polygala amarella</u>

YEAR	SITE	Total No. Plants	No. flowering	No. of Fruits	Total No. of Seeds	Estimated No. Seeds/100 Plants
1969	Widdybank Fell	75	39	161	242	323
	Cronkley Fell	60	11	38	57	95
1970	Widdybank Fell	226	27	403	685	303
	Cronkley Fell	119	11	103	175	147
1971	Widdybank Fell	210	35	308	554	264
	Cronkley Fell	112	19	158	284	254
1972	Widdybank Fell	183	34	228	410	224
	Cronkley Fell	83	19	106	191	230

Unfortunately, although observations suggest that seed germination occurs in the year following seed-set, it was not possible to determine whether viable seed was stored in the soil. Thus it is not known whether the apparently high seed production in 1969, 1970 and 1971, but low germination in the years 1970, 1971 and 1972, reflects a loss of seed (potential new plants) to the population.

A smaller number of seeds was produced on Cronkley Fell than on Widdybank Fell in 1969 and 1970, but in the other two years approximately the same number were produced on both Fells. The lower values for the individuals on Cronkley Fell are reflected to some extent by a lower rate of recruitment for the individuals in quadrat 10.2 over the four years.

SECTION 7: SPECIES BIOLOGY

Polygala amarella is a short-lived perennial which overwinters as a rosette which frequently becomes purple. Plants which flowered remained healthy over the Winter period, often not dying until the Spring growth started in other plants. (See Figures 24 and 25 where the behaviour of the individuals in quadrats 6.1 and 7.2 is shown). Of 46 plants which flowered in 1969 and survived to the Autumn of the same year, 16 were lost over the following Winter period. Fifteen of those which remained survived and went on to flower again, some in several successive years.

Plants established from seedlings were able to flower under natural conditions on Widdybank Fell in their second year. Although, of approximately 300 seedlings recorded in 1969, only one of the surviving 150 individuals flowered in 1970. A further 13 of these plants flowered in 1971 and 25 in 1972. This number of plants which appeared as seedlings and flowered within the study period was much greater than for Viola rupestris and Viola riviniana. For these species only a few seedlings in Upper Teesdale reached maturity and flowered within the four years.

Flowering began in mid-May and was continuous throughout the season, finishing about mid-September. Fruits were still being formed at that time, although any buds which were present usually aborted. In 1970, the cold Spring delayed the start of flowering; large numbers of flowers did not appear until mid-May. However, the apparently favourable season which followed allowed the more vigorous plants on Widdybank Fell to continue to flower into early October.

Germination was observed throughout the growing season (May to September) although the pattern of germination was different in the four years. In 1969, there was an abrupt burst of germination in July in each of the quadrats. In 1970, seedlings occurred throughout the season and the greatest number appeared during the Summer months. In 1971 and 1972 germination occurred in the Spring and Summer seasons with very few appearing in the Autumn.

Seed collected from Widdybank Fell on 7th July, 1970, and sown in Durham two days later, germinated within eight weeks. (Only a minimum sample of 30 capsules, each from separate plants, was collected because of the very small and restricted population on the Fell). The seed was sown in John Innes seed compost and placed in an unheated greenhouse. Eleven seedlings appeared over a period of 30 days from 2nd September to 5th October, 1970, 9 of which survived. In 1971 all the seeds from a small sample of seed from both the blue and pink-flowered plants germinated within one month of sowing at Durham University.

A careful watch was kept on the Fells for seedlings from newly fallen seed. Although seed could be seen lying near flowering individuals, no germination was observed throughout the fruiting period. The evidence of a large number of seedlings in 1969 around a plant which flowered in 1968, but before it produced fruit in 1969, indicates that germination takes place in the year after seed is set. As seed germinated within several weeks at Durham some delaying mechanism may have operated on Widdybank Fell. This could have been environmental, or the result of a seed dormancy mechanism, or a combination of both; ~~compare~~ Newman (1963).

Pollination is by insects or self, Knuth (1906/1909), although Fearn (1971) states in the majority of cases self-pollination occurs automatically.

The mean number of fruits per flowering plant and the mean number of seeds per capsule is given in Table f ± standard error. The number of fruits varied considerably both between the two populations on Widdybank and Cronkley Fells and between years. The best year for the production of fruits was 1970 when a much greater number were recorded, on average, for each flowering than in the other years. This difference was most pronounced for the results for Widdybank Fell. The lowest value was recorded in 1969 for both the pink-flowered population on Cronkley Fell and the blue-flowered population on Widdybank Fell.

Plants on Widdybank Fell were more vigorous than those on Cronkley Fell, a fact which is indicated by the higher mean number of

Table f

FRUIT AND SEED PRODUCTION

(MEAN PER FLOWERING PLANT; MEAN PER FRUIT)

Polygala amarella

YEAR	SITE	Fruits	Seeds/Capsule
1969	Widdybank Fell	4.13 ± 1.86	1.5 ± 0.13
	Cronkley Fell	3.43 ± 0.72	-
1970	Widdybank Fell	14.93 ± 3.80	1.7 ± 0.15
	Cronkley Fell	9.32 ± 1.17	-
1971	Widdybank Fell	8.80 ± 1.60	1.8 ± 0.16
	Cronkley Fell	8.00 ± 1.11	-
1972	Widdybank Fell	7.50 ± 0.80	1.8 ± 0.16
	Cronkley Fell	5.60 ± 0.50	1.9 ± 0.16

Figures for flower and fruit production are given as a mean per flowering plant ± standard error. The mean number of seeds/capsule is also given ± standard error

(Data are not available for Cronkley Fell except in 1972) fruits produced per flowering plant on Widdybank Fell in all but 1971. The results suggest that this difference in production was due to environmental factors such as exposure or grazing rather than to anything linked to the genetically controlled colour factor. The population of plants with blue flowers growing on Cronkley Fell would be expected to have mean values comparable with the Widdybank Fell population if any genetically controlled factor was responsible for the less vigorous nature of the pink-flowered plants. However, in fact, in the two years for which data were recorded for Cronkley Fell blue-flowered plants, the mean value of 7.00 ± 1.37 in 1971 was lower than that obtained for the other population on Widdybank Fell, and in 1972 the mean value of 8.00 ± 1.70 was higher. This population was very restricted and the number of flowering plants sampled in the two years was small.

Dispersal of seed in this species was very restricted. Observation of seedlings close to a plant which flowered in the previous year suggests that the relatively large, heavy seed falls close to the parent plant. It is possible that scattered individuals resulted from animal dispersal. Polygala vulgaris has two oil bodies (elaiosomes) known to attract ants which may move the seeds, Ridley (1930). Polygala amarella has these structures which may act in a similar way.

SECTION 8: LIFE STRATEGY

Polygala amarella on both Widdybank and Cronkley Fells is a short-lived perennial species which reproduces entirely by the production of seed. There is no indication that there was a greater risk of mortality of the newly germinated seedlings and, in fact, the overall mortality of plants in their first year at 29 per 100 plants was slightly lower than that for plants over one year old, which was 31 per 100 plants in the population. Thus throughout the life of the individual mortality was independent of the age of the plant.

Plants produced approximately 200 to 300 seeds per 100 individuals annually in the populations recorded on Widdybank and Cronkley Fells, and in all years the number of potential new plants (seeds) was far greater than the loss through mortality. The overall annual figure of 239 seeds per 100 plants shows that there were eight times as many seeds produced as individuals that were lost.

Despite this, in 1971 and 1972 the number of seedlings recorded entering the population did not outweigh the number of plants that were lost, and only in 1969 were substantial numbers of seedlings observed. The importance of the high recruitment in 1969 to the maintenance of the total population is clearly shown by the curves in Figure 21, which all rise steeply between Autumn 1969 and Spring 1970, when the surviving seedlings of 1969 were included in the values for the total population. Without this high level of recruitment in 1969 all the quadrat populations would have shown a fairly steep decline over the four years.

The germination and establishment of seed is the most important period in the life cycle for this and many other species which reproduce by means of seed production. The rate of seed germination may be determined by environmental factors acting firstly on the production of seeds by the parent plants, and secondly on the ability of the seed to germinate and become established. Once germination had taken place the risk of mortality appeared to have been no greater than for mature plants. Thus the most important periods in the life cycle of this species are the seed production and germination phases, and it is clear from the results that environmental constraints do affect these in such a way as to prevent the replacement rate being achieved in some years.

The reasons for the low recruitment rates in 1970, 1971 and 1972, or indeed the very high recruitment in 1969, are difficult to determine. During the four-year study the rate of seed production was not greatly different for each of the years. For the very high recruitment of seedlings in 1969 to be the result of seed production in the previous year, the actual rate of production would need to have been approximately five times the annual figure recorded in the four years' study. This would represent a production rate of 1,200 seeds per 100 plants in the population assuming the proportion of seed not germinating in the year following seed-set was the same in the period 1968 to 1969 as in the other years. It seems likely, therefore, that the very high recruitment in 1969 was due to environmental factors affecting the ability of the seeds to germinate since the required rate of seed production is very high.

Almost 100% viability was obtained for seeds collected on Widdybank Fell and sown at Durham University in 1971. If this level of germination were achieved on the Fell in 1969 and the rate of seed production in 1968 was similar to the annual rate recorded for the period 1969 to 1972, then only 240 seedlings would have been recorded per 100 plants present in the population. Thus for the recruitment rate of 222 seedlings per 100 plants observed on Widdybank Fell in 1969 to be achieved almost 100% germination of 1968 seed must have occurred, or viable seed had been retained in the soil from other years and conditions were favourable for its germination in 1969, or high rate of flowering in 1968

Clearly the fact that some individuals were able to survive for several years, during which time they flowered and set seed in a number of years, is important to the population in overcoming periods when recruitment is low. In addition it is possible that viable seed may remain in the soil providing a reservoir from which recruitment can take place in seasons favourable to germination. Although seed collected on Widdybank Fell germinated within eight weeks when sown in Durham immediately after collection, germination on the Fell occurred in the year following seed-set. Thus there would appear to be some environmentally imposed dormancy which, if it acted over a number of years, could have resulted in a reservoir of seed being retained in the soil.

Plants normally began flowering in their third year, although many seedlings of 1969 did not flower until their fourth year, and many more had not flowered by the end of the study period. Thus it took several years for plants to develop to the flowering stage after which they were able to flower in successive years. A few mature plants flowered in all four years of the study.

The life strategy of this species is very similar to that reported by Rabotnov (1960) for Trifolium pratense growing in a sub-alpine meadow. Unlike the same species growing on flood plain meadows which were usually monocarpic, these plants were polycarpic. Plants which were established from seed did not flower until they were 5 to 10 years old, flowering thereafter in some cases in the succeeding years, and a few plants reached 20 years of age. Polygala amarella does not appear to be quite as long-lived as Trifolium pratense and seed production and recruitment were higher than for Trifolium pratense.

The populations of Polygala amarella on Widdybank and Cronkley Fells were very restricted and no doubt this reflects the rigours attached to the successful dispersal and germination of seed. There is no dispersal mechanism in this species, and the large heavy seed did not germinate far from the parent plant. Seed was able to germinate in the closed sugar limestone turf and on both Fells seedlings and mature plants were observed growing in close proximity to Calluna vulgaris. Thus interspecific competition would not appear to be restricting the population to any great extent.

Over the four years of the study the annual rate of seedling recruitment was 54 per 100 plants, and with an annual mortality rate of 30 per 100 plants, the potential for expansion was not great. However, there was a slight increase between Autumn 1968 and Autumn 1972 in the number of individuals in the quadrats, although this only represented a 5% increase in the original populations. The restricted nature of these populations in Upper Teesdale seems to be related to the relatively low* reproductive potential of the species, to the much lower rate of germination in most years, and to the lack of any dispersal mechanism for the seed. Fearn (1971) also considered the low colonising

---

* Although the rate of production of seeds was much higher than for Viola rupestris or Viola riviniana, when compared with the rate of seed production in Draba incana which also has no method of vegetative reproduction, the rate was low.

ability of Polygala amarella was due to the small number of large heavy seeds.

At another site in Yorkshire plants were much more vigorous, more widespread and present in relatively large numbers in a grassland habitat similar to that in Upper Teesdale. No doubt the environmental conditions experienced by the plants in this area, which is both at a lower altitude and further south than Upper Teesdale, were less severe. It is possible, therefore, that a greater number of seeds are produced at this lower site allowing a larger population to be maintained than in Teesdale.

The long-term survival of this species through the Forest maximum does not present any particular problem. If, as the evidence from pollen analysis suggests, Turner et al. (1973), the sugar limestone soils supported an open forest, this species would have been able to survive. Pigott (1956) suggests that the late glacial flora could have survived under these conditions and, in fact, that Polygala amarella was 'noted in fruit under small openings in the canopy of sub-alpine Picea abies forest in the Alps'.

Clearly the populations of this species in Teesdale, at the present time, by virtue of their very restricted nature, are very vulnerable. Although grazing does not appear to have any great impact on the reproductive ability of the species, any increased stocking rate would give cause for concern. The most obvious threat is from collection, not only of mature plants but also of seeds. Thus any requirement for seed or plants for research purposes should be carefully considered. Loss of large numbers of potential plants (seeds) in a year when seed production was high could have a devastating long-term effect on the population, which, because of the plants' low reproductive performance and low recruitment, would take many years to rectify.

Figure 21

TOTAL POPULATIONS

Polygala amarella

FIGURE 21

TOTAL POPULATION – Polygala amarella

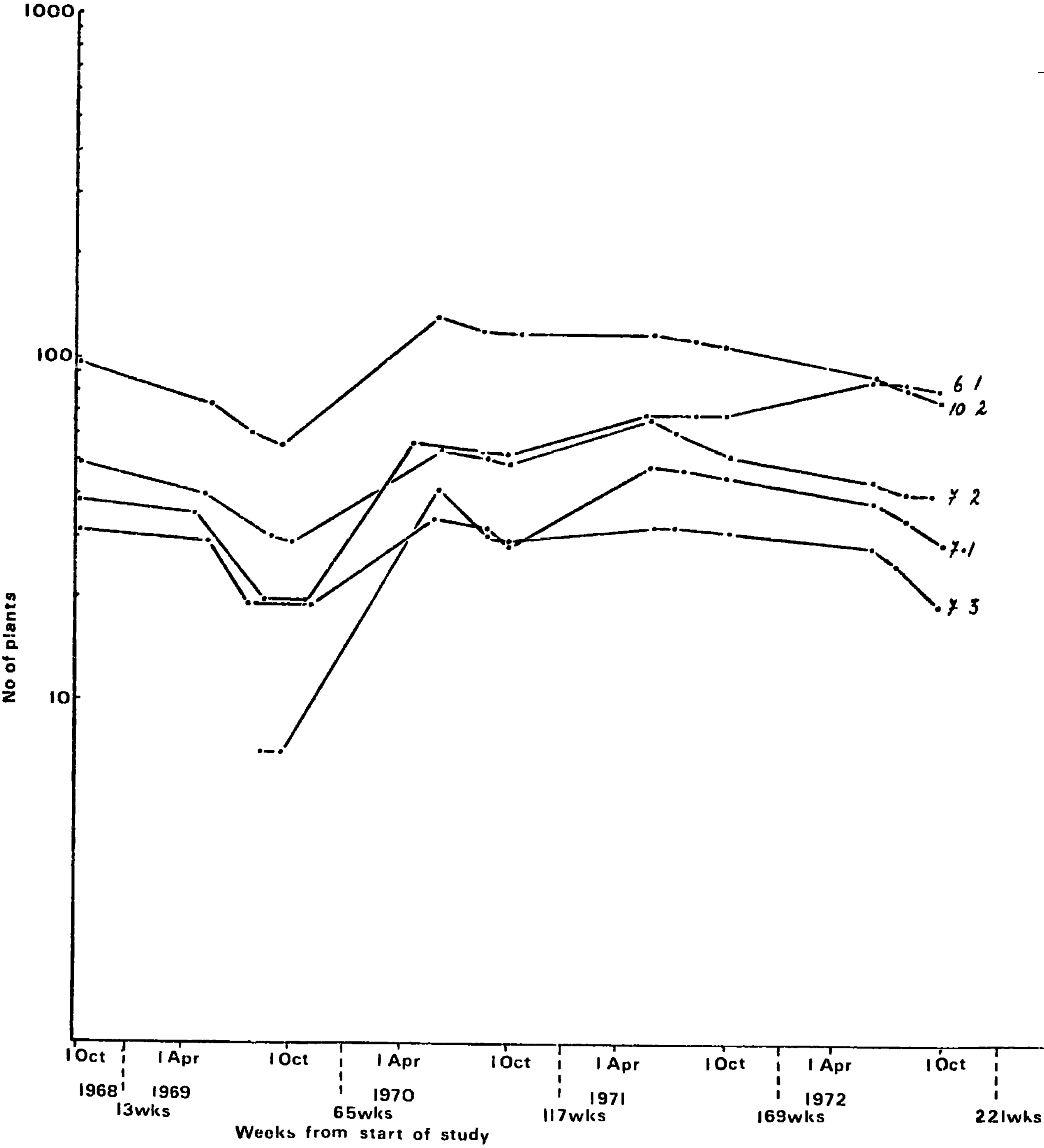


Figure 22

SURVIVORSHIP CURVES OF MIXED-AGE POPULATIONS

Polygala amarella

FIGURE 22

SURVIVORSHIP curves of mixed-age populations- *Polygala amarella*

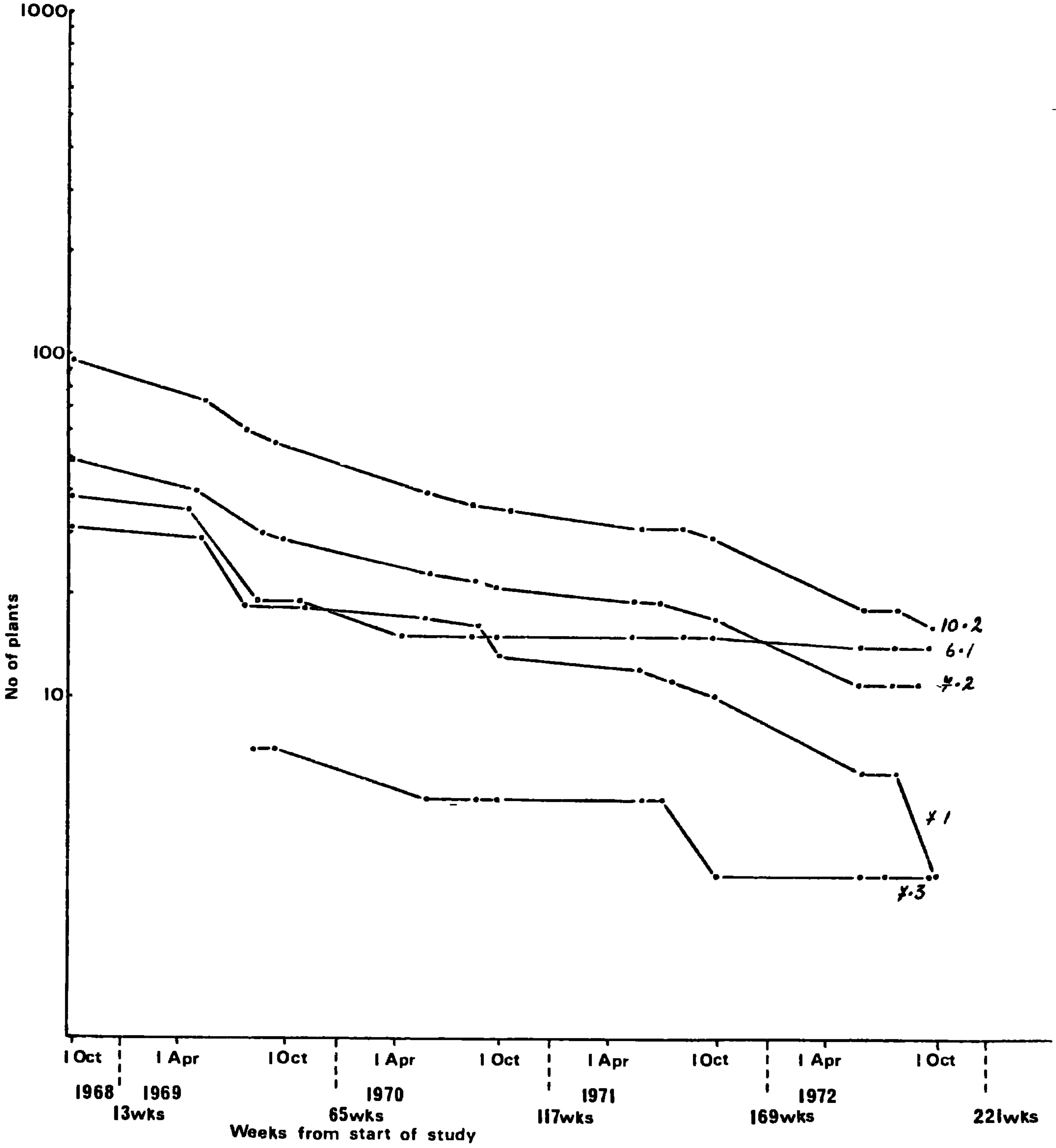


Figure 23

SURVIVORSHIP CURVES OF SEEDLINGS
'BORN' AT THE SAME TIME

Polygala amarella

FIGURE 23

SURVIVORSHIP curves of seedlings born at the same time – *Polygala amarella*

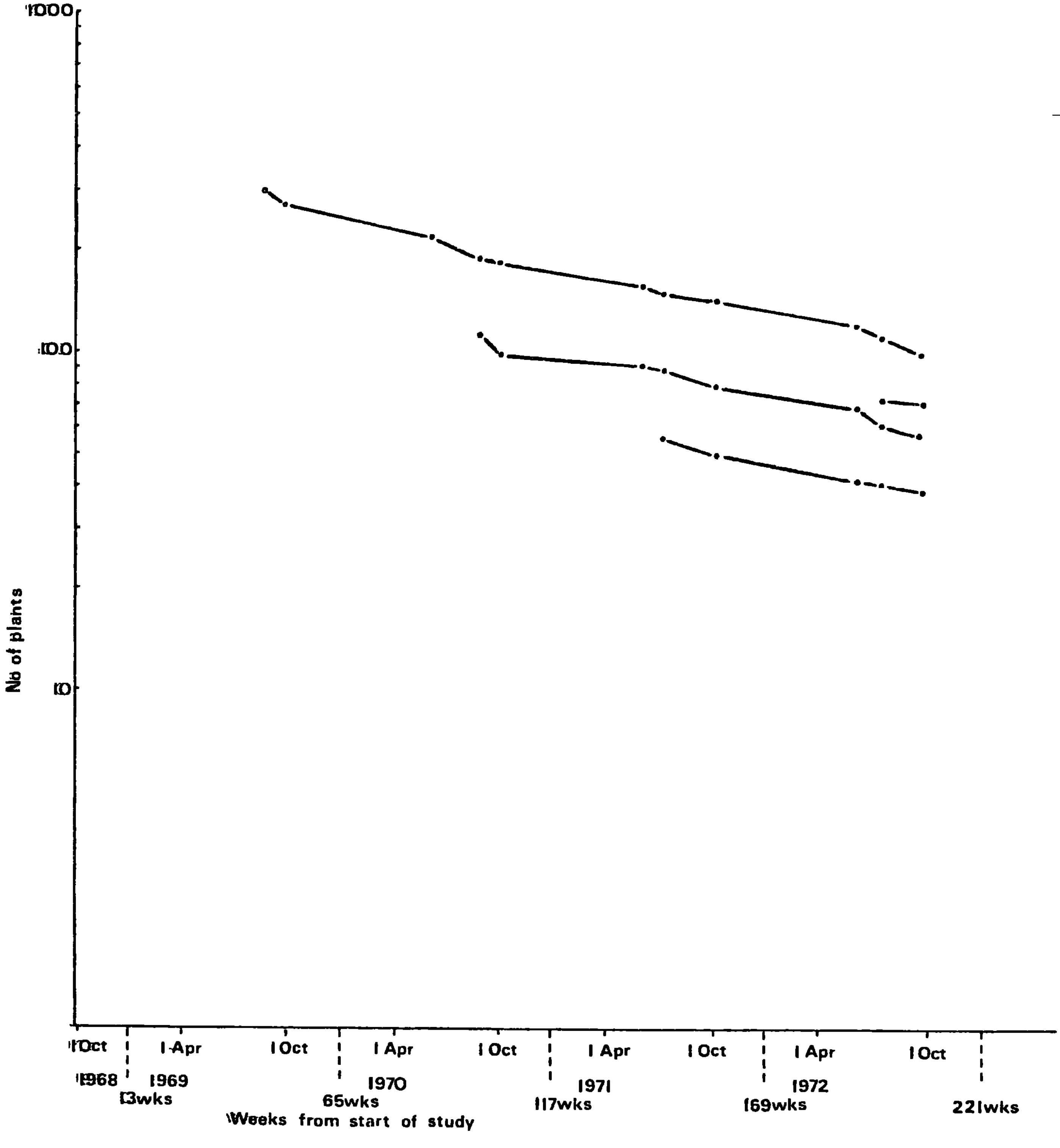


Figure 24

BEHAVIOUR OF INDIVIDUALS IN QUADRAT 6.1

Polygala amarella

FIGURE 24 Behaviour of individuals in quadrat 6·1 - *Polygala amarella.*

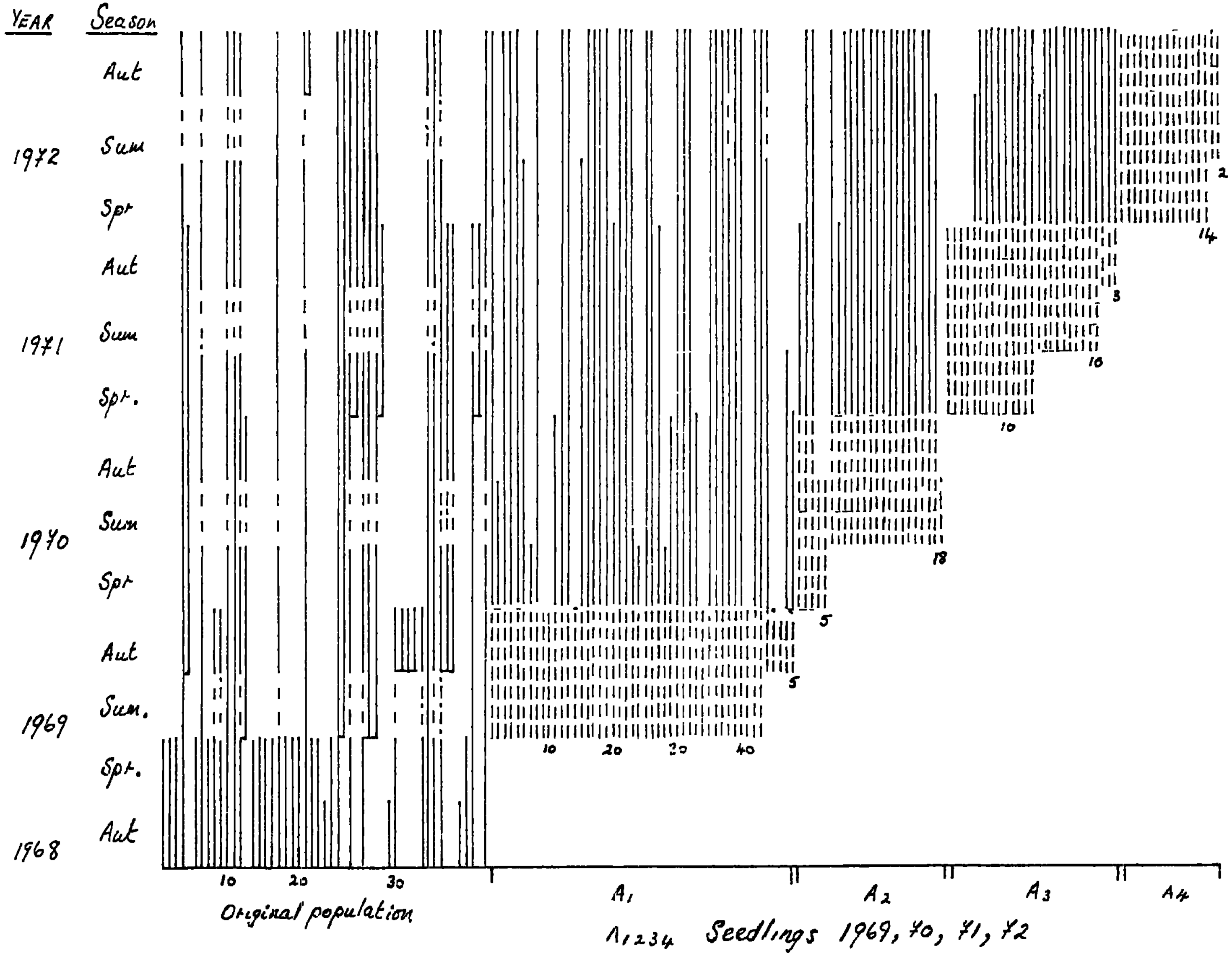
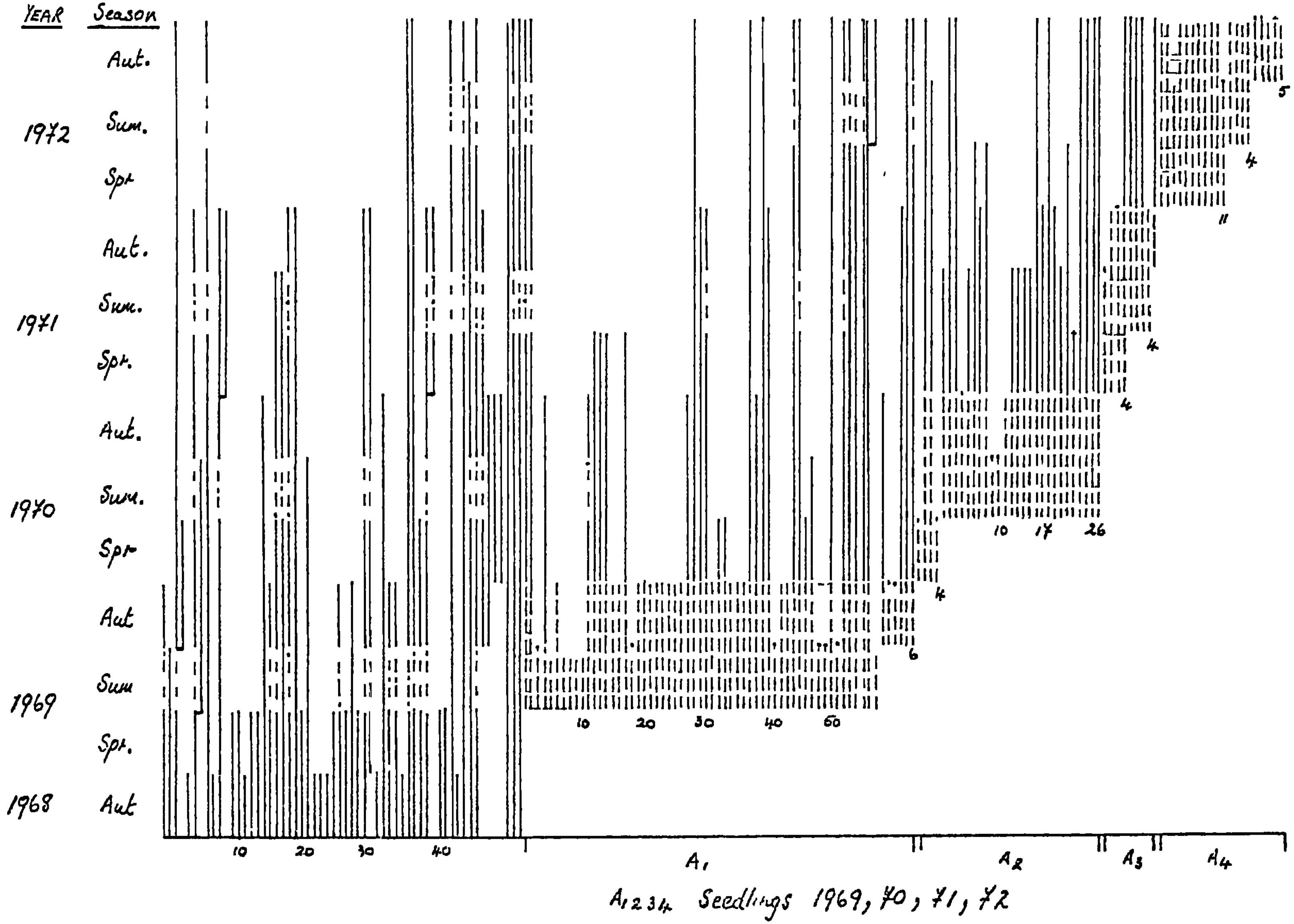


Figure 25

BEHAVIOUR OF INDIVIDUALS IN QUADRAT 7.2

Polygala amarella

FIGURE 25 Behaviour of individuals in quadrat 7·2 - *Polygala amarella*



CHAPTER EIGHT

DRABA INCANA

SECTION 1: INTRODUCTION

Draba incana is a short-lived, usually mono-carpic perennial, which reproduces entirely by the production and germination of seed and the subsequent establishment of seedlings. The individual or 'unit of reproduction' is considered to be any plant which develops from a seed. Usually this plant has a single rosette, although occasionally after flowering, or because the rosette was partially eaten or damaged, subsidiary rosettes were formed on the original stem-stock. (One plant, whose inflorescence and part of the rosette was eaten in 1970, produced 10 new rosettes on the remains of the original one later in the season).

Sometimes, a woody stem bore two or more rosettes, but none of the axillary rosettes produced separate rooting systems and were, therefore, not treated as separate individuals. These axillary rosettes are shown by branching lines in Figures 30 and 31, which show the behaviour of the individuals in quadrats 7.3 and 8.1.

Draba incana occurs on both Widdybank and Cronkley Fells, but exclusively on open, eroding limestone or in areas where the turf is periodically disturbed, such as at site 2 where moles were active, at least, during the study period. It is clear that the species cannot tolerate competition. Seedlings which are very small germinated in large numbers, often at a relatively high density. In the early stages of establishment mortality was high, with dense groups of seedlings undergoing self-thinning.

Clapham, Tutin and Warburg indicates that in Europe this species is biennial to perennial. In Upper Teesdale, perhaps because of the cold, bleak climate, Draba incana acts as a perennial. Plants take a number of years to develop to the stage when they flower, producing a large number of seeds and then usually dying. The seed which was produced during the study germinated in the Spring of the following year although occasional seedlings were observed in the Autumn.

The survival of this species depends on plants being able to produce a large number of seeds, which require areas of bare soil for germination, and seedling establishment. Draba incana is a species which takes advantage of any areas where the habitat is open, such as on rock-ledges and eroding sugar limestone. The production of large numbers of seed ensures that the species is able to colonise newly exposed surfaces, a necessary prerequisite for any plant growing on unstable or open substrates.

SECTION 2: PERMANENT QUADRATS

The populations of Draba incana were restricted on Widdybank and Cronkley Fells to areas of open eroding sugar limestone, and soils derived from the sugar limestone which had been disturbed by moles. Four permanent quadrats were established at four different sites on Widdybank Fell and, in addition, records of flowering performance were made on Cronkley Fell. Site 2 was situated close to the reservoir's edge, sites 5 and 7 at 200 to 250 metres and site 8 at more than 500 metres from top water-line.

Quadrat 2.1 was situated in an area where moles were active. The vegetation cover in a sample metre is shown in Figure 26 and it can be seen from this that a very large proportion of the area is bare ground, created by destruction of the turf by moles. The intact vegetation was dominated by *Sesleria caerulea* and *Festuca ovina* with *Thymus drucei*, *Carex flacca*, *Carex caryophyllea*, *Carex panicea*, *Minuartia verna* and *Koeleria gracilis*.

Quadrat 5.1 was situated in an extremely exposed area of eroding sugar limestone with a very sparse population of *Draba incana*. Where vegetation cover existed it was restricted to small tussocks of *Festuca ovina*, *Sesleria caerulea*, *Minuartia verna*, *Thymus drucei* and *Plantago maritima* often in single species stands. *Linum catharticum* and *Gentianella amarella* were also present.

Quadrat 7.3 was also recorded for *Polygala amarella* which was present together with *Draba incana* in the moss/lichen substrate overlying bare rock. *Calluna vulgaris* was present at the edge of the quadrat with *Rhacomitrium lanuginosum*, *Ctenidium molluscum* and *Cladonia spp* in the moss/lichen layer.

Quadrat 8.1 was very open with a large area of bare limestone in which the *Draba incana* plants flourished. *Sesleria caerulea*, *Festuca ovina* and *Carex ericetorum* were present in part of the quadrat where *Draba incana* was absent. On the open areas of limestone, tufts of *Festuca ovina*, *Helianthemum chamaecistus*, *Minuartia verna* and *Thymus drucei* wore present.

Figure 26

MAP OF VEGETATION IN QUADRAT 2.1

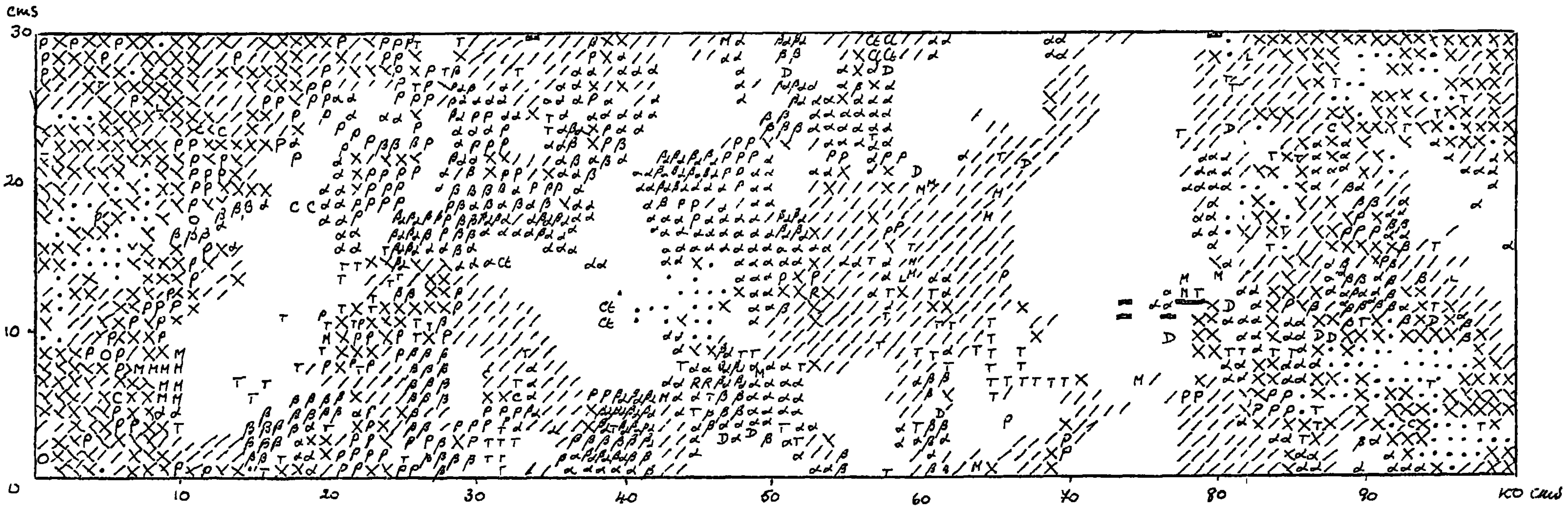
Draba incana

FIGURE 26 Map of vegetation in quadrat 2·1 - Draba incana (June 1970)

KEY to main species : · Sesleria caerulea, / Festuca ovina, P Carex panicea,

T Thymus drucei, ▬ Koeleria gracilis, α moss cover,

β lichen, D Draba incana



Records of flowering performance were made inside an exclosure on Cronkley Fell. Here the plants were growing on very open, bare sugar limestone which had been exposed as a result of soil erosion initiated by rabbits burrowing in the shallow soil. Sheep rubbing along the collapsed burrows followed by wind erosion caused large areas of turf to be completely destroyed.

Sample sites were established close to quadrats 2.1 and 8.1. However, at the other sites the populations of Draba incana were very restricted and there were very few additional plants outside the permanent quadrats.

SECTION 3: POPULATION FLUX

There was great variation in the total number of individuals in each permanent quadrat over the period of recording. However, with the exception of quadrat 8.1, where there was a decrease of 29% in the total number of individuals, the number of plants in quadrats 2.1, 7.3 and 5.1 increased by 47%, 245% and 311% respectively.

Seedlings have not been included in the figure for the total population until they were one year old, that is, seedlings germinating in the Spring of one year are only counted as being part of the population in Spring of the following year. The inclusion of these individuals is clearly shown by the sharp increase in the total populations between the Autumn and Spring records of 1969/1970 and 1970/1971 (Figure 27). This increase reflects the high rate of recruitment of seedlings in the Springs of 1969 and 1970 respectively.

(Seedlings of Draba incana showed a very high rate of mortality during the first few months following their appearance in the quadrats. It is for this reason that they have not been included in the population until their second year. Although the surviving seedlings were not mature, they had by then developed into a small rosette and had overcome the most difficult period of establishment. A similar reasoning was used when deciding not to include seedlings less than one year old in the figures for total populations for the other species which produced seeds. The seedlings for these species did not show any increased risk of mortality during their first year, no doubt due to the relatively large size of the seed and the persistence of the large cotyledons. However, during this first year plants were clearly not able to make a contribution to the replacement of the population).

The curves for the total populations of quadrats 2.1 and 5.1 show a particularly large rise in the Springs of 1970 and 1971, as a result of high seedling recruitment in 1969 and 1970 and their subsequent survival. The curve for quadrat 7.3 shows that there was a step-wise increase in the number of plants in all three years. For quadrat 8.1 increases in the total number of plants over the years 1969 to 1970 and 1970 to 1971 were followed by a decrease in the final year of this study, such that there was an overall decline in the total number of individuals, between Autumn 1968 and Autumn 1972.

Survivorship curves for the individuals in the originally recorded mixed-age population are shown in Figure 28. The steep gradients of each of these curves indicate that the rate of mortality was high. Inspection of the curves shows that mortality occurred largely during the growing season, with the latter part of the Summer, particularly for quadrats 2.1 and 7.3, showing the greatest losses. This increased rate of mortality was no doubt linked to the death of mature individuals, following flowering.

Half-life values (Table a) based on the decay of the original population, give an indication of the actual rate of loss of individual plants, more than one year old, from the quadrat. These figures show that it would probably take six years for complete replacement of the population, and that only a few individual plants may live this long. Since the plants are usually mono-carpic, a few plants may take this long to develop sufficiently to flower and set seed.

Although in Draba incana mortality was not independent of age, being concentrated in the early stages of seedling establishment (Section 5), the equation used to calculate half-life values for the other species has been utilised here. Since the mixed-age populations did not include seedlings and the curves are approximately linear, it was considered appropriate to use this formula.

SECTION 4: SEASONAL SURVIVAL AND ANNUAL RECRUITMENT

Seasonal survival varies considerably both between quadrats and between years. The lowest seasonal value was obtained from the individuals in quadrat 5.3 during the Summer of 1969; the highest value being recorded for quadrat 7.3 over the Winter period Autumn 1969 to Spring 1970. The individual figures represent the proportion of individuals surviving over each six-month period, expressed as a rate per individual present at the beginning of each time interval. For this species the number of

Table a

HALF-LIFE VALUES

Draba incana

Quadrat	Half-life (years)	No.
2.1	2.7	62
7.3	3.1	40
8.1	3.2	102

Quadrat 5.1 - Only 9 individuals were originally recorded in Spring 1969 and these had all disappeared 2½ years later

No. - Number of individuals in the originally recorded mixed-age population

plants 'at risk' does not include seedlings, that is, plants less than one year old, but does include all other plants surviving at the time of recording,(Table b).

When comparisons are made between the values for each of the seasons it is clear that the rate of survival of individuals over the Summer period 1969 was much lower than for any other seasons. These figures are all statistically significantly different at the 5% level of probability. The value for the Summer season of 1970 is also statistically different at the 5% level of probability when compared with the Winter figures,except that obtained for the period Winter 1971/1972. Although the differences are not statistically significant,the Summer survival rates for 1971 and 1972 were also lower than all the Winter values except 1971/1972. These results illustrate that mortality, particularly during the growing seasons of 1969 and 1970, was high. As was indicated in the previous section, this high rate of mortality may be linked to the death of individuals following flowering.

The survival rates for the quadrats are not statistically significantly different from each other at the 5% level of probability.

Seedling recruitment for <u>Draba incana</u> in all quadrats and years was high when compared with the other species. The figures shown in Table c show the rate of appearance of seedlings in each of the quadrats for each of the years, expressed as a rate per individual present in the quadrats in the Spring. The differences between the rates of recruitment in the quadrats were not large. However, the figures for 1970 and 1972 show that recruitment in these years was higher than in 1971. Note that in 1969 seedlings were not recorded until the Autumn when they were

Table b

SEASONAL SURVIVAL

Draba incana

SEASON	QUADRAT 2.1	5.1	7.3	8.1	
Winter 1968/69	0.95	No record	0.98	0.82	0.89 ± 0.02
Summer 1969	0.61	0.44	0.54	0.50	0.54 ± 0.04
Winter 1969/70	0.78	0.50	1.00	0.93	0.87 ± 0.03
Summer 1970	0.66	0.93	0.69	0.86	0.77 ± 0.03
Winter 1970/71	0.91	0.85	0.83	0.92	0.88 ± 0.02
Summer 1971	0.83	0.91	0.82	0.81	0.83 ± 0.02
Winter 1971/72	0.77	0.76	0.81	0.84	0.80 ± 0.02
Summer 1972	0.81	0.92	0.85	0.74	0.82 ± 0.02
	0.79 ± 0.02	0.84 ± 0.03	0.81 ± 0.02	0.79 ± 0.02	

Overall seasonal survival for each quadrat population both between quadrats and between season is shown ± standard error

Table c

ANNUAL SEEDLING RECRUITMENT

Draba-incana

QUADRAT

YEAR	2.1	5.1	7.3	8.1	
1969**	1.17	6.75	2.33	1.14	1.61**
1970	3.52	1.07	3.31	1.87	2.61*
1971	0.50	2.16	1.50	0.40	0.91*
1972	1.60	1.21	No record	2.97	2.08*
	1.46*	1.56*	2.14*	1.60*	

* Figures shown with an asterisk represent the annual recruitment rates for the summed totals of each quadrat and year (1970 to 1972)

** Note: in 1969 seedlings were not recorded until the Autumn when they were approximately six months old approximately six months old (seedlings were only first identified in the Autumn of 1969). Recruitment in that year was probably also high since a large number of seedlings die in the first few months.

Clearly in all the years seedling recruitment was much greater than the annual loss of plants, being approximately 38 in every 100 plants over one year old, present in the quadrats. Even in 1971 when only 91 seedlings per 100 plants were recorded, this represents a rate of recruitment over twice the rate of loss.

The largest individual ~~value~~ rate was obtained for the individuals in quadrat 5.3 in 1969, and since the plants were six months old when they were recorded the actual rate for germinating seedlings was probably much higher. The figure gives some indication of the ability of Draba incana to take advantage of suitable open conditions. In this quadrat there were very few mature plants, in fact in the Autumn of 1969 only 4 were present, and from these few a relatively large number of seedlings appeared as a result of seed germination.

The lowest individual value was recorded in 1971 for the plants in quadrat 8.1. Here, the annual rate of loss of individual plants was only just compensated for by recruitment. However, the number of plants surviving to enter the population as one year old plants, was well below the replacement rate. Although recruitment in other years was high enough to more than compensate for the loss of plants, as has already been indicated the total population decreased over the study period.

SECTION 5: AGE-SPECIFIC SURVIVAL AND AGE-DISTRIBUTION

Survivorship curves for groups of individuals 'born'* at the same time show that mortality was dependent on the age of the individual. The curves represent the rate of loss of seedlings appearing in each quadrat, which have been summed for each year (Figure 29). For the groups of seedlings recorded in 1970, 1971 and 1972, the curves show that mortality was concentrated in the first few months following germination. Where data are available (seedlings of 1970 and 1971) it is clear that the rate of mortality dropped from the Autumn of the year of germination and remained relatively low thereafter.

The curve for the 1969 seedlings is also remarkably linear. Individuals were not recorded until after the period when there was the greatest risk of mortality. The curve conforms very closely to Deevey (1947) type 2 which indicates that mortality is a continuing risk throughout the plant's life. However, despite this, it is clear that mortality is not independent of the age of the individual and the other survivorship curves conform very closely to Deevey (1947) type 3, which indicates that the risk of mortality is greatest during the early part of an individual's life.

There is no indication in the curves that there was a period in the life-cycle when the majority of plants flowered and died, resulting

---

* Born in this context is used to indicate the appearance of a seedling in the quadrat

in a rapid decline in the survivorship curves. Plants did not flower until their third year (Figures 30 and 31), and then not all of them did so. The evidence suggests that it takes three or more years for an individual to reach maturity and flower. The plants which flowered invariably died, often in the Autumn of the same year. This loss is shown by the increased rate of mortality, indicated by the curves in Figure 28, over the Summer to Autumn period.

It appears that following the initial stages of seedling establishment, mortality in the first and second year is brought about by environmental factors acting on the individual. In subsequent years mortality is related largely to whether a plant flowers or not, although individuals did die without flowering.

In a species which is mono-carpic it might have been expected that there would be one year in which the majority of plants from one cohort flowered and died. This was not, however, observed during the four years of the study and only a relatively few plants (1969 seedlings) flowered in their third year. It may be advantageous to the species that individual plants should attain maturity and flower at different ages. In this way the population does not have to rely, as do annuals and biennials, on successful seed-set in each year.

The proportion of the different age-groups in each of the quadrat populations, at the end of the study period, varied a great deal (Table d). Only a very small number of the plants were more than 3½ years old. Since none of the plants had flowered and all had reached the age at which flowering can occur, they were clearly important to the survival of the quadrat populations. Plants 'born' in 1970 could also be of

Table d

DISTRIBUTION OF AGE-CLASSES IN

EACH QUADRAT AT THE END OF THE STUDY PERIOD

<u>Draba incana</u>

	AGE IN YEARS	QUADRAT 2.1	5.1	7.3	8.1
Present Autumn 1968	4	6	0	5	14
'Born' Spring 1969	3½	11	12	21	22
'Born' Spring 1970	2½	64	17	55	31
'Born' Spring 1971	1½	10	6	57	5
'Born' Spring 1972	1	85	13	No record	74

'Born' is used in this context to indicate that a seedling was recorded in the quadrat considerable importance to the replenishment of the population as they too were nearing the age when they were able to flower.

The small number of older plants reflects the high rate of mortality of the individuals. Although there were relatively few surviving seedlings from 1971, except in quadrat 7.3, overall there was a high proportion of plants which had not reached maturity. The small number of 1971 seedlings which survived to Autumn 1972 was partly due to the fact that fewer were recorded and partly to their higher mortality.

SECTION 6: REPRODUCTIVE PERFORMANCE

The reproductive performance of this species, expressed in terms of the number of seeds produced per 100 individuals present in each of the sites, was high. The data in Tables e and f show the total number of plants in each quadrat and sample site, together with the number flowering and the estimated number of fruits and seeds.

The figures for site 2 include data from quadrat 2.1 and sample site 2ssl, and for site 8 data are included from quadrat 8.1 and sample site 8ssl. There were no sample sites associated with permanent quadrats 5.3 and 7.3 because of the very restricted nature of the population of Draba incana in these areas, and therefore, there is insufficient data to provide a comparable estimate of fruit and seed production. The figures for Cronkley Fell have been obtained from a sample recorded on a very exposed area of eroding sugar limestone, within a sheep and rabbit-proof exclosure. The mean number of fruits per flowering plant and seeds per capsule used in calculating these figures are shown in Section 7, Table g.

Table e

ESTIMATED PRODUCTION OF SEEDS BETWEEN SITES

Draba incana

SITE	Total No. Plants	No. flowering	No. of Fruits	Total No. of Seeds	Estimated No. Seeds/100 Plants
2	689	83	614	11,420	1,660
8	673	78	780	14,898	2,210
Cronkley Fell	424	93	1,255	24,106	5,690

Table f

ESTIMATED PRODUCTION OF SEEDS BETWEEN YEARS

Draba incana

YEAR	Total No. Plants	No. flowering	No. of Fruits	Total No. of Seeds	Estimated No. Seeds/100 Plants
1969	148	17	170	3,230	2,180
1970	402	80	800	14,640	3,640
1971	625	101	1,010	20,099	3,220
1972	610	56	610	11,407	1,870

The production of seeds, which represent the potential new plants, was much greater on Cronkley Fell than for the two sites on Widdybank Fell (Table e). It is likely that this greater rate of seed production was related to the much more open conditions experienced by the plants on Cronkley Fell, where there was almost no other competing vegetation. By comparison the rate of seed production at site 2 was low. At this site *Draba incana* survived in small pockets of open sugar limestone soil exposed by moles. However, there was more vegetation in close proximity to the individual plants of *Draba incana* and this may have restricted the ability of plants to fruit and set seed. The quadrat and sample site at site 8 contained a more open vegetation than site 2, although not as open as on Cronkley Fell, and this is perhaps reflected by the intermediate figure for seed production obtained for that site.

The differences in the production of seed when comparisons are made between years (Table f) are less marked than those between sites. Clearly 1970 and 1971 were the years in which most seed was produced; however, whether this was due to more favourable climatic conditions or to the fact that more plants attained maturity, and were able to flower is not known.

It is probable that the number of plants reaching maturity and flowering was more important in determining the rate of seed production in any one year. This will depend on many factors affecting the rate of germination, the subsequent survival of the seedlings and their development to flowering. Clearly a large cohort whose survival rate was high would make a large contribution to seed production in the year in which they flower.

The very high rate of seed production recorded for this species was clearly essential when the rigours attached to seedling survival and establishment were so great. The very small seed also appeared to suffer a high rate of mortality. From an annual rate of production of 2,541 seeds per 100 plants, only 157 seedlings per 100 plants were recorded during the study.

SECTION 7: SPECIES BIOLOGY

Draba incana is a short-lived perennial species which only flowers once, and then dies. Individuals occurred as a rosette of leaves, singly or in small groups, and were sometimes well-scattered. All plants were restricted to the very few open areas of eroding sugar limestone, or exposed soil.

Dense groups of young plants were often found near the dead remains of the flowering plants of the previous year. Self-thinning took place within some of these groups in their first year. Sometimes there was a gradual decline in the number of seedlings, although more often the decline over the first six months was quite steep. In 1970 a group of 70 seedlings recorded in the first week of June had completely disappeared by the first week of August.

In Teesdale, plants were all perennial, although Clapham, Tutin and Warburg indicate that it is a biennial to perennial. Plants grown in Durham from seed collected on Widdybank Fell in 1968, germinated in January 1969 and flowered in the same year (within seven months). These plants did not die, but flowered again in 1970 after which they all died.

Also, under natural conditions at Durham University, seed collected on Widdybank Fell in 1970 and sown in pots, germinated in the Autumn of that year and flowered in the following year. These plants, despite the short period of development, had all attained a size approximately equal to that of plants which flowered in Upper Teesdale.

Plants from naturally sown seed, which germinated on Widdybank Fell, developed into very small rosettes in the first season and grew only slowly in the following years. This slow development probably prevented plants in Teesdale from flowering in their first year (Figures 30 and 31). It seems quite likely that restrictions imposed on the development of plants by the severe climate cause a normally biennial species to behave as a mono-carpic perennial.

Plants began to flower in mid-May and continued until mid-September; ripe fruits were formed from mid-July until late into September on Widdybank Fell. Seed was shed throughout this period and later. Flowering occurred at about the same time for plants grown from seed under natural conditions at Durham University. Here, fruits developed more quickly, at least in 1972, when in mid-July plants on Widdybank Fell were beginning to produce ripe fruits, most fruits in Durham had dehisced.

Germination occurred on Widdybank Fell in early Spring; in mid-April in 1969, 1971 and 1972, but not until the first week in May in 1970 when April was very cold. In 1970 a few seedlings were observed on Widdybank Fell at site 2 in October, indicating that exceptionally, germination can take place in the Autumn.

At Durham University seed collected in Teesdale and sown in transplanted turf from Widdybank Fell in the Autumn of the same year, germinated the following year, some two to three weeks before seedlings were first observed in Teesdale. However, germination in the Autumn of the year seed was set, occurred more readily in Durham. In the Autumn of 1970, plants from Widdybank Fell were transplanted* to Durham. These plants flowered and set seed in 1971, and the seed germinated in the late Summer of that year.

Seed collected on Widdybank Fell and sown indoors on petri-dishes also germinated in the Autumn of the same year it was produced. Since germination only occurred, under natural conditions in Upper Teesdale, very occasionally in the Autumn of the year seed was set, it appears that environmental conditions impose a period of dormancy on the seed. Germination was thus delayed until the Spring of the following year.

Flowers of <u>Draba incana</u> were fully self-compatible and almost totally inbreeding, Fearn (1971).

Both the number of fruits per flowering plant and the number of seeds per capsule was large when compared with the other species included in the study. The mean number of fruits per flowering plant at sites 2, 8 and Cronkley Fell show differences which are related to the openness of the habitat in which the plants were growing. Plants

---

* All the plants which were collected from Widdybank Fell and transplanted were from the area below the projected top-water-line of the reservoir

growing in openings created in the sugar limestone turf by moles, produced fewer fruits per flowering plant in each of the years than at the other sites, (Table g).

The mean number of seeds per capsule, recorded at each of the sites, shows little variation either between site or between the years. This result suggests that the environmental factors affecting the reproductive performance of this species in Upper Teesdale at the different sites (Section 6) act on the rate of production of fruits.

Fruit and seed production for groups of plants either transplanted from Widdybank Fell or grown from seed in Durham, indicate that climate played an important role in determining the rate at which fruits and seeds were formed. In 1971, the number of fruits per flowering plant was recorded for three groups of plants; details of the results are given below:

(1) Plants transplanted from Widdybank Fell to an ash pit on Widdybank Fell - 8.90 ± 1.42

(2) Plants transplanted from Widdybank Fell to Durham University - 18.90 ± 1.45

(3) Plants germinated and grown at Durham University - 39.30 ± 1.57

These results clearly illustrate the effect of climate on fruit production, with the lowest figure being obtained for the plants grown on Widdybank Fell. The very high mean number of fruits per flowering plant recorded for plants sown and grown at Durham University, suggest that the temperature may also affect fruit production by influencing the rate of development of a plant. Thus plants which grew more slowly in their first year or two in Teesdale (transplanted from Widdybank Fell), flowered and produced relatively high numbers of fruits. However, this number was much lower than that recorded for the plants whose rate of development from the seedling stage had been very rapid (plants sown and grown in Durham).

The rate of seed production per capsule was also greater for those plants transplanted from Widdybank Fell and grown in Durham. The figures for groups (2) and (3) above were 22.80 ± 0.84 and 25.80 ± 0.81 respectively. Although the differences between these figures and those obtained on Widdybank Fell are not large, they do show that under the more favourable climatic conditions of lowland Durham a greater number of seeds per capsule were produced.

Seed dispersal was limited to a small area around the parent plant. The seed was very light, (mean weight 0.16 mg.), and may, therefore, have been scattered by the wind, although seed remained attached to the septum for some time.

Wider dispersal was achieved when plants were uprooted. Some plants with ripe fruits fell over when the tap root was exposed by soil erosion, caused by wind and rain. Often, the plant was completely uprooted and blown some distance away. Sheep also uprooted flowering plants which had both ripe and unripe capsules, and these were sometimes moved some distance. The unripe capsules often matured after the plant had been moved.

Table g

FRUIT AND SEED PRODUCTION

(MEAN PER FLOWERING PLANT; MEAN PER CAPSULE)

Draba incana

YEAR	SITE	Fruits/ flowering plant	Seeds/capsule
1970	2	7.75 ± 0.87	18.30 ± 1.15
	8	9.44 ± 0.98	18.24 ± 0.56
	Cronkley Fell	12.82 ± 0.97	18.27 ± 0.89
1971	2	7.27 ± 0.57	19.53 ± 0.56
	8	10.98 ± 1.23	20.26 ± 0.71
	Cronkley Fell	11.80 ± 1.21	19.93 ± 0.50
1972	2	7.20 ± 0.55	18.00 ± 0.92
	8	9.63 ± 0.85	18.73 ± 0.81
	Cronkley Fell	15.78 ± 1.34	19.26 ± 0.50

Figures for fruit production are given as a mean per flowering plant ± standard error. The mean number of seeds per capsule is also given ± standard error

SECTION 8: LIFE STRATEGY

This mono-carpic perennial relies entirely on the production of seed, its germination and establishment for survival. The species is intolerant of competition, growing exclusively in areas where there is a bare sugar limestone substrate or where the soil has been exposed. The evidence from this study suggests that interspecific competition may cause a reduction in the ability of the plants to flower and set seed in this last situation.

Annual mortality of the species was high, with approximately 40% of the population over one year of age dying annually. This figure varied from year to year and quadrat to quadrat reaching 61% in quadrat 2.1 over the Winter period 1969/1970. This rapid rate of decay in the number of individuals was more than compensated for by the annual recruitment of seedlings which was 157 per 100 plants present in the population.

A very high rate of recruitment is essential for a species where mortality is high. However, the figure quoted above for annual mortality was based on the rate of decay of individuals over one year old. There was a much greater risk of mortality in the early stages of seedling establishment; 63% of the seedlings died in their first year. Clearly, with seedling mortality this high, recruitment must also be very high in order to ensure that sufficient plants survive to reach maturity and produce the seed for the next generation.

Seedlings took some time to develop to maturity and flower on both Widdybank Fell and Cronkley Fell. No seedlings were observed to flower in their second year, however plants did flower in their third year (Figures 30 and 31). Note that in these figures where the behaviour of the quadrat populations 7.3 and 8.1 are shown, seedlings (broken line) are not included until the Autumn when the surviving plants were nearly six months old. It appears that the climatic conditions retarded the development of the plants. In more favourable conditions at Durham University, plants flowered in their second year. Unlike the results obtained by Rabotnov (1960) where for Trifolium pratense the life strategy was changed by climatic conditions, from that of a short-lived big-bang producer to a much longer lived repeating producer, the more extreme climatic conditions in Teesdale slow down the rate at which plants reach maturity and flower.

For this species it has been possible to estimate, for each permanent quadrat, the amount of seed produced and relate this to the rate of recruitment observed in the following year. The number of plants flowering, the number of seeds they produced and the number of seedlings recorded in the quadrat the following Spring are shown in Table h.

Clearly, there was a very high rate of loss of potential new individuals (seeds) between seed-set and germination. The figures indicate that up to 90% of the seed failed to germinate in the year following seed-set. This loss of potential recruits to the population may have been brought about by a variety of factors. Although almost 100% viability was obtained for seed collected in Teesdale and sown in Durham, some of the seed produced on the Fell in some of the years may have been non-viable. Seed may also have been destroyed by animals or disease, and even more was probably dispersed outside the quadrat. A

Table h

REPRODUCTIVE PERFORMANCE AND SEEDLING RECRUITMENT IN THE SPRING OF THE FOLLOWING YEAR FOR EACH PERMANENT QUADRAT

<u>*Draba incana*</u>

QUADRAT	YEAR	No. flowering Plants	Total No. Fruits	Total No. Seeds	Seedlings
2.1	1969	11	55	1,023	229 in 1970
	1970	0	0	0	77 in 1971
	1971	17	78	1,450	179 in 1972
5.3	1969	5	69	1,311	30 in 1970
	1970	1	38	722	97 in 1971
	1971	1	8	152	46 in 1972
7.3	1969	9	71	1,349	222 in 1970
	1970	9	79	1,501	185 in 1971
	1971	No record			
8.1	1969	6	55	1,045	159 in 1970
	1970	3	30	570	53 in 1971
	1971	16	128	2,432	288 in 1972

few seeds may also have lain dormant in the soil, although the percentage germination obtained when seed was sown artificially suggests that this involved very few seeds. In 1970 no fruits were produced in quadrat 2.1 and yet seedlings were observed in the following year. This result suggests that seed was blown or carried into the quadrat or that some seed does in fact lie dormant in the soil. Clearly, the latter would be very advantageous, allowing seedlings to appear in reasonable numbers in years following seasons when seed-set was low. However, as yet there is no evidence that seed was stored in the soil.

Draba incana is dependent for its survival on having a very high reproductive potential. In this way the population is able to ensure that the rigours attached to germination and establishment of seedlings, which have been shown to be very severe, are overcome. A large number of potential new plants are produced, many of which never germinate. The small seedlings also suffer a very high risk of mortality during the early stages of establishment and relatively few survive and go on to flower and set seed. Approximately 80% to 90% of the seeds which were produced failed to germinate, annually a further 63 seedlings in every 100 died in their first year and thereafter plants were lost at an annual rate of 38 per 100. These figures clearly illustrate the selective forces acting upon this species and indicate that for every 1,000 seeds which were produced only 8 survived to become three-year old plants (the age at which flowering first occurs in Upper Teesdale).

This strategy is important for a species which is sensitive to competition and only able to survive under very open or unstable conditions. A large number of potential plants must be produced to enable the species to exploit new situations created by erosion or other activities, such as disturbance by moles.

The most critical period for the survival of Draba incana in Upper Teesdale was during the forest maximum, when competition was probably at its most severe. For the species to have survived, exposed areas of soil or bare sugar limestone must have been present throughout. It is quite likely that moles may have been very important in this respect, when wind and rain erosion would have been reduced by the presence of the open forest, Clark, in Valentine (1965).

Figure 27

TOTAL POPULATION

<u>Draba incana</u>

FIGURE 27

TOTAL POPULATION - Draba incana

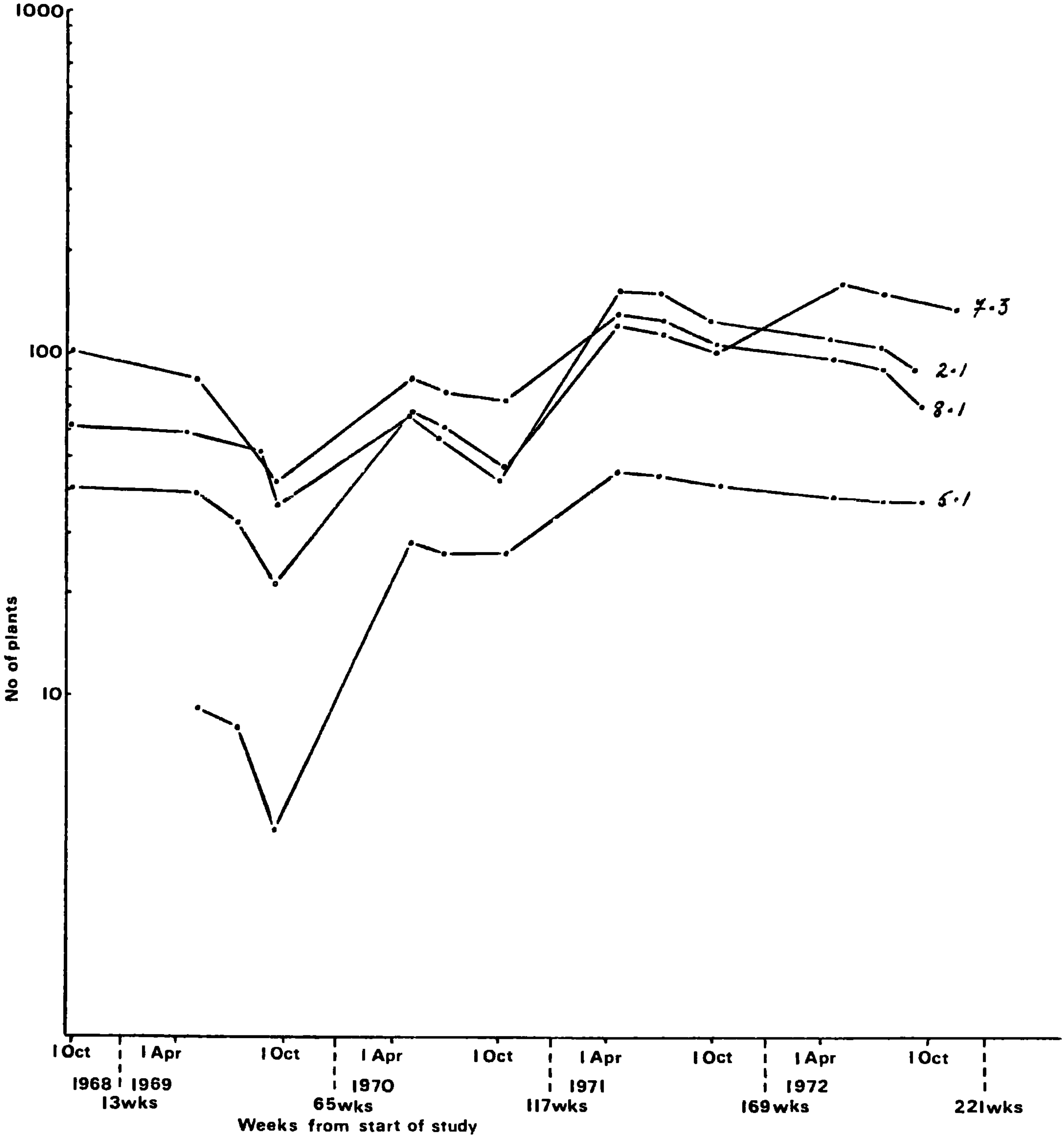


Figure 28

SURVIVORSHIP CURVES OF MIXED-AGE POPULATIONS

Draba incana

FIGURE 28

SURVIVORSHIP curves of mixed age populations–Draba incana

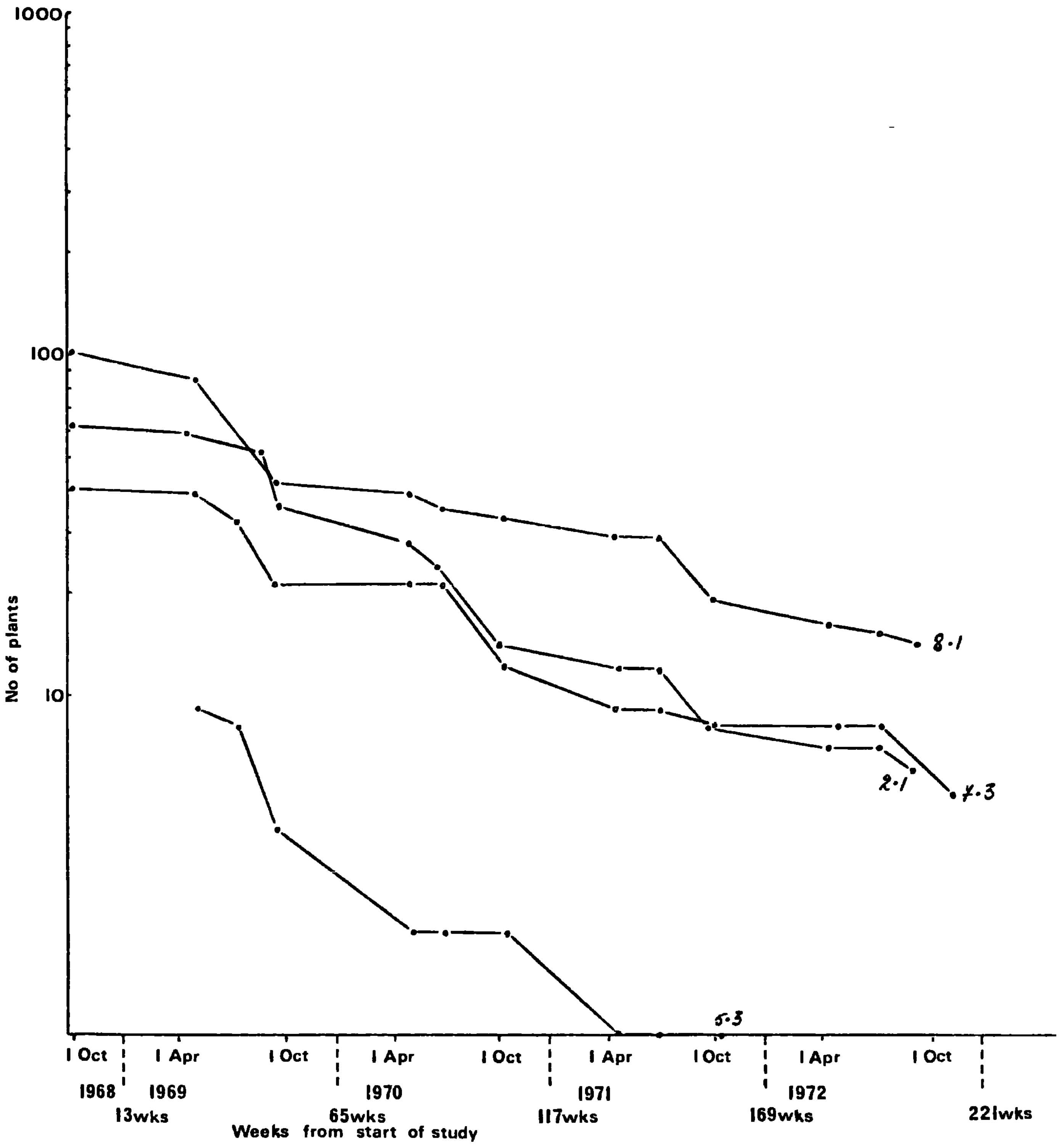


Figure 29

SURVIVORSHIP CURVES OF SEEDLINGS

'BORN' AT THE SAME TIME

Draba incana

FIGURE 29

SURVIVORSHIP curves of seedlings born at the same time – *Draba incana*

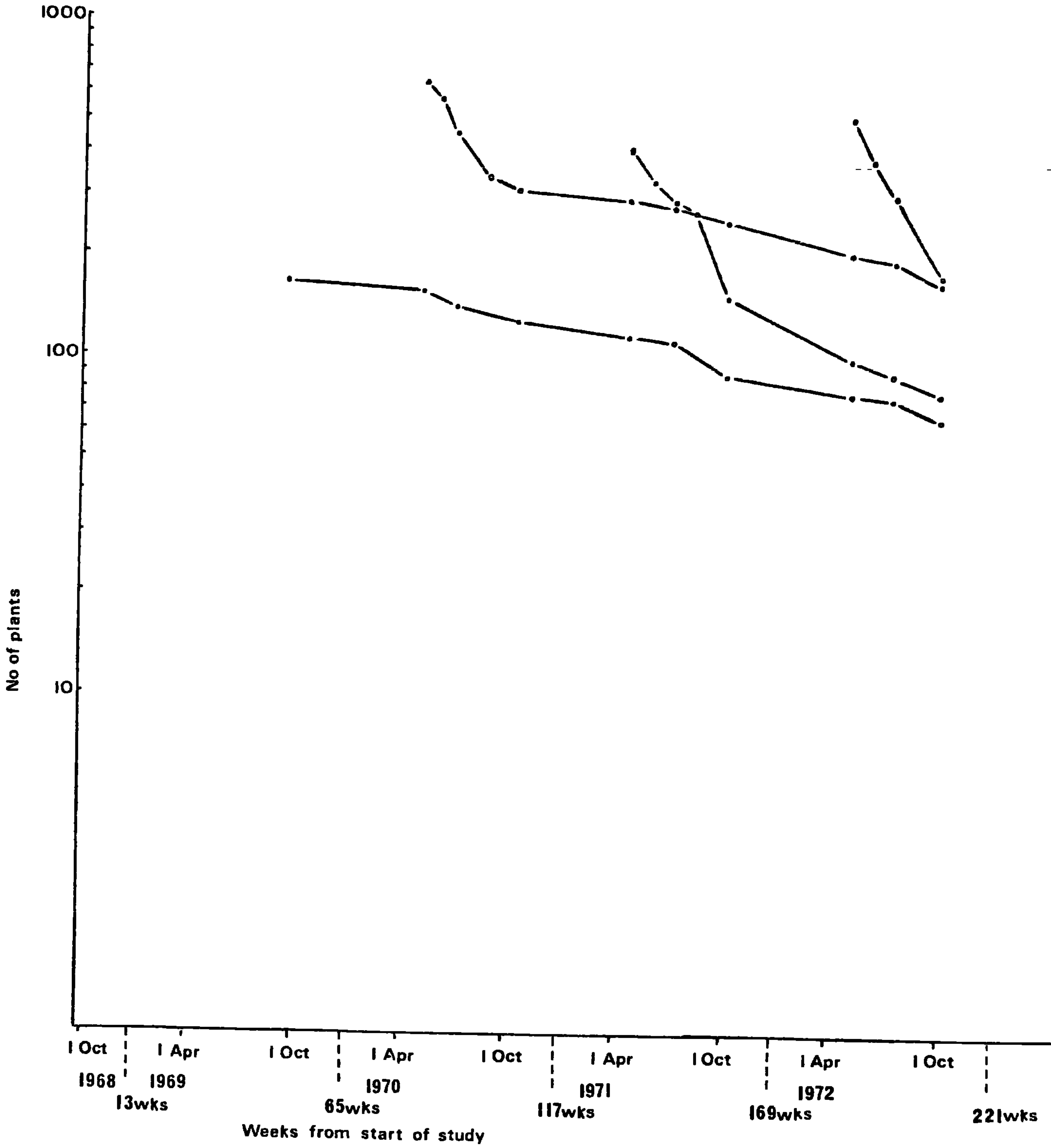
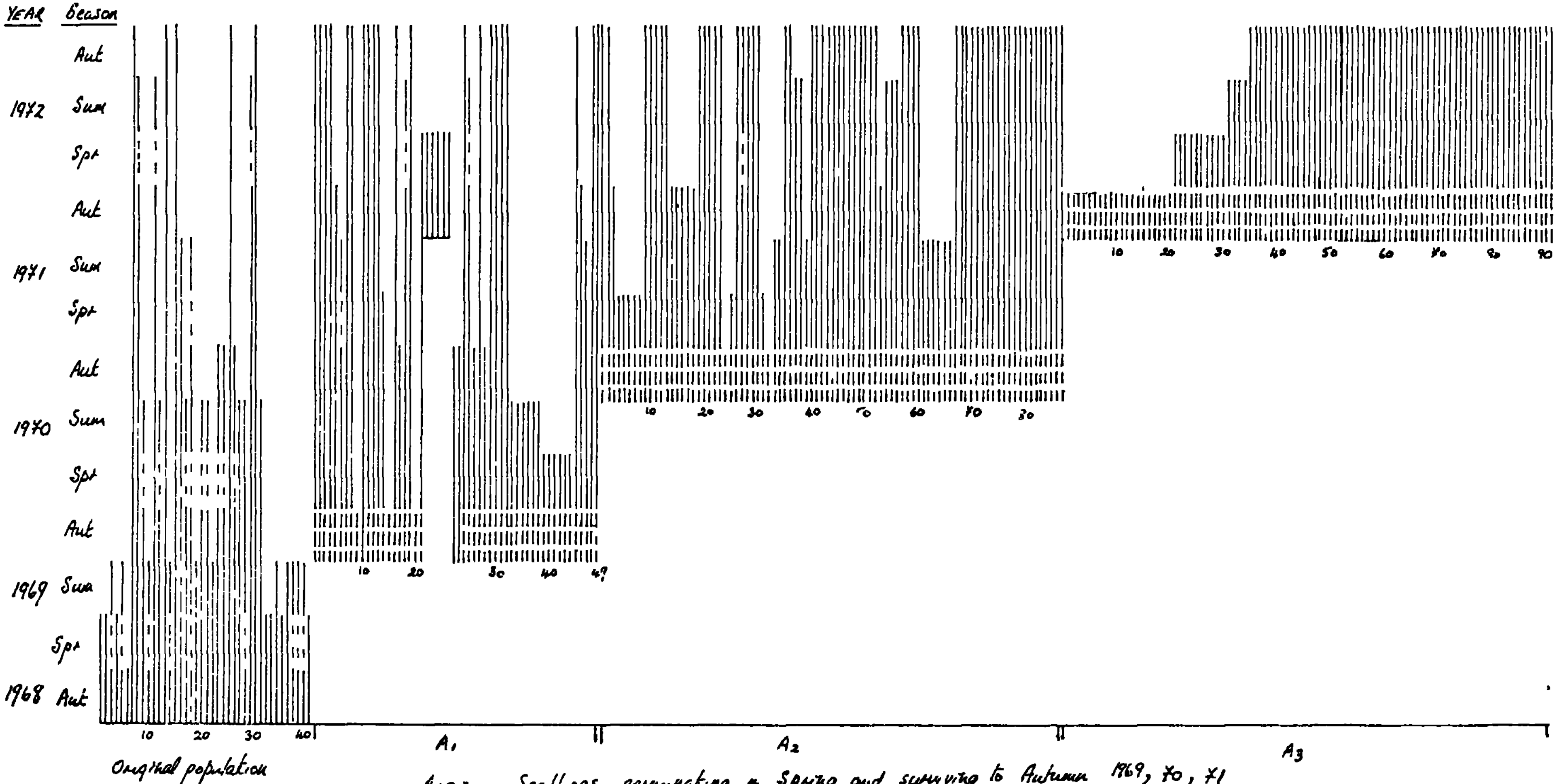


Figure 30

BEHAVIOUR OF INDIVIDUALS IN QUADRAT 7.3

Draba incana

FIGURE 30 Behaviour of individuals in quadrat 7 3 - <u>Draba incana</u>



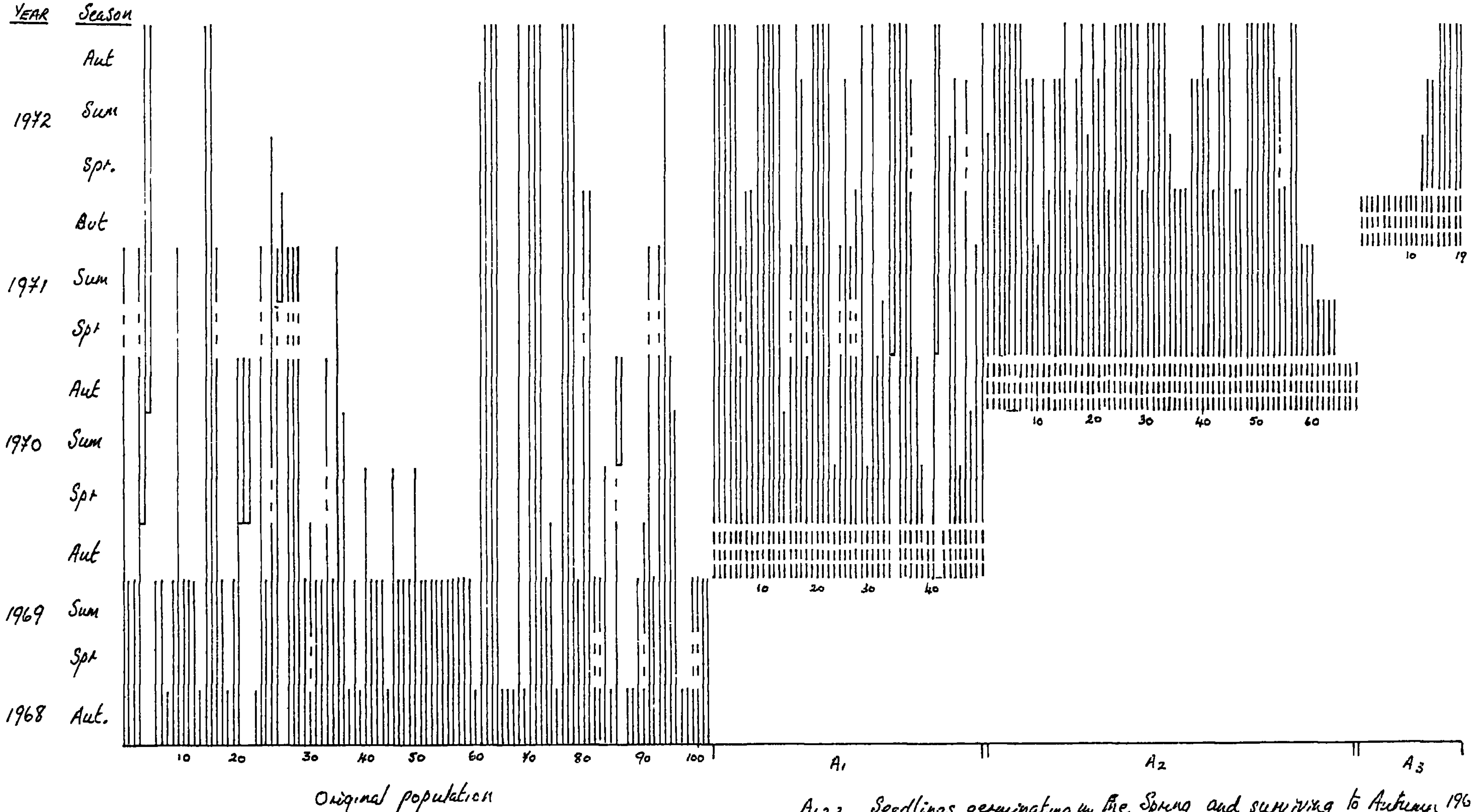
A123 Seedlings germinating in Spring and surviving to Autumn 1969, 70, 71

Figure 31

BEHAVIOUR OF INDIVIDUALS IN QUADRAT 8.1

Draba incana

FIGURE 31 Behaviour of individuals in quadrat 8 1 - Draba incana.



A1,2,3 Seedlings germinating in the Spring and surviving to Autumn 1969, 70, 71

CHAPTER NINE

GENTIANA VERNA

SECTION 1: INTRODUCTION

Gentiana verna is a small perennial herb which produces fine underground stolons each terminating in a rosette of leaves. In the field it is impossible to separate the ramifications and rosettes arising from any individual plant. Therefore, in this study each rosette is regarded as an individual reproductive unit in the population (equivalent to an individual in an animal species).

Individual plants are relatively short-lived, only occasionally surviving if they have flowered. Plants which do flower seldom set seed in Upper Teesdale as few capsules reach maturity because of predation by sheep on Widdybank Fell, and sheep and rabbits on Cronkley Fell. Despite the relatively high rate of mortality and inability of the species to set seed, the total population over the period of study showed an increase in numbers. This increase was brought about entirely by the production of new vegetative shoots arising from the underground stolons.

These underground stolons are from 2 to 15 cm. long, simple or branched and grow just below the ground surface. Rosettes usually die without flowering a second time (see Figures 36 and 37) and leave a short underground stock from which stolons and adventitious roots arise. The same process of development may then be repeated by the secondary rosettes, Elkington (1963).

SECTION 2: PERMANENT QUADRATS

For the purposes of studying Gentiana verna six permanent quadrats were established as six different sites, five on Widdybank Fell and one on Cronkley Fell, in an exclosure which was sheep proof and mostly rabbit proof. On Widdybank Fell the quadrats were situated in heavily grazed, closed sugar limestone turf. An example of the type of vegetation is indicated by the chart showing the dominant species present in part of quadrat 1.1 (Figure 32). Three of the quadrats on Widdybank Fell contained Calluna vulgaris and were situated in the intermediate zone where the sugar limestone turf and heather grassland ~~moor~~ merge. Further details of the vegetation in the quadrats are given below.

Quadrat 1.1 had an almost completely closed cover with Festuca ovina dominant in the sward. The vegetation of the second metre length of this quadrat is shown in Figure 32. Kobresia simpliciuscula and Calluna vulgaris were completely absent but Carex panicea, Carex flacca, Campanula rotundifolia, Linum catharticum, Plantago maritima, Briza media, Galium sterneri, Selaginella selaginoides, Prunella vulgaris and Koeleria gracilis were present in 1970 when the vegetation in the quadrat was mapped.

Quadrat 4.1 had a vegetation cover which was completely closed and apparently heavily grazed. Sesleria caerulea and Festuca ovina were the dominant species in the sward. Both Calluna vulgaris, which almost completely dominated a small part of the quadrat, and Kobresia simpliciuscula were present together with Carex flacca, Potentilla erecta, Campanula rotundifolia, Antennaria dioica, Thymus drucei, Polygonum viviparum and Selaginella selaginoides.

Quadrat 7.2 was almost completely dominated by *Sesleria caerulea* and *Festuca ovina*. *Helianthemum chamaecistus*, *Hieracium pilosella*, *Lotus corniculatus* and the mosses *Dicranum scoparium* and *Rhacomitrium lanuginosum* were present although *Kobresia simpliciuscula* and *Calluna vulgaris* were absent. This quadrat was also recorded for *Polygala amarella*.

Quadrat 8.3 had both *Calluna vulgaris* and *Kobresia simpliciuscula* in a very closed sward, close to a sheep track. *Polygala serpyllifolia*, *Thalictrum alpinum*, *Selaginella selaginoides*, *Carex flacca* and *Potentilla erecta* were also present.

Quadrat 8B.1 was situated in an area where *Calluna vulgaris* was present together with *Empetrum nigrum*. Most of the quadrat was dominated by *Sesleria/Festuca* turf with *Viola rupestris*, *Kobresia simpliciuscula*, *Briza media*, *Campanula rotundifolia*, *Thymus drucei*, *Viola lutea*, *Polygonum viviparum* and *Koeleria gracilis*.

Quadrat 10.1 on Cronkley Fell had a closed sward dominated by *Sesleria caerulea* and *Festuca ovina*. This quadrat was situated inside an exclosure and although it was not possible to keep rabbits out entirely, there was very little grazing over the period of recording.

Each permanent quadrat had a sample site associated with it, the details of which are given in Chapter three.

SECTION 3: POPULATION FLUX

The total number of individuals in each of the permanent quadrats remained over the period of study at or above the number recorded when

Figure 32

MAP OF VEGETATION IN QUADRAT 1.1

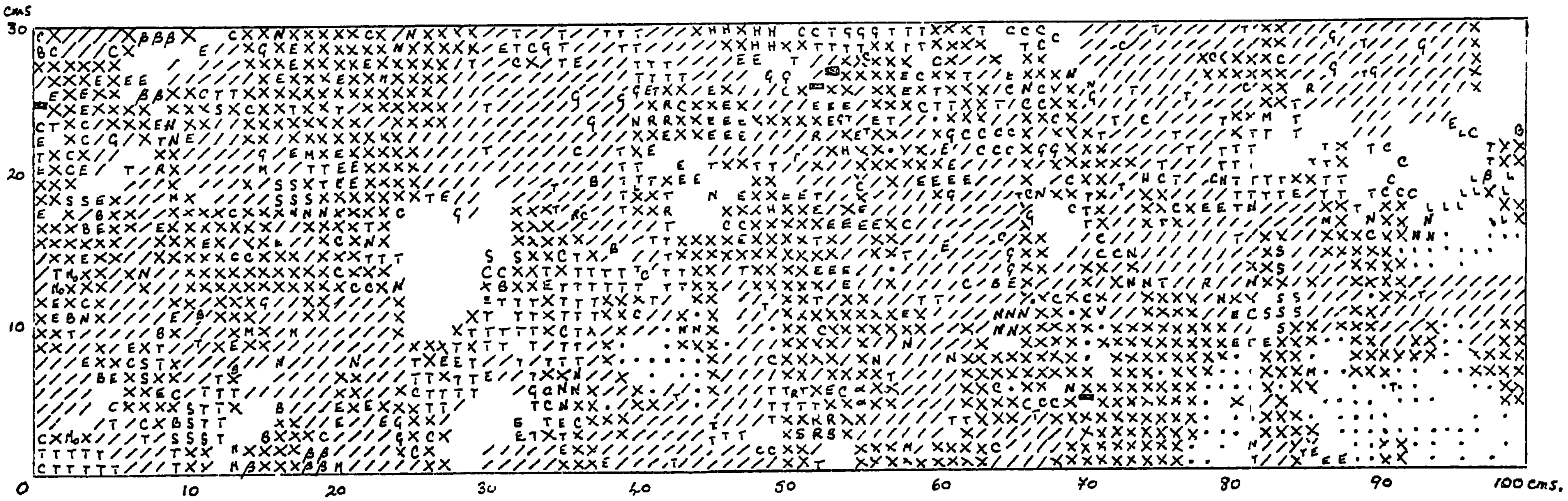
Gentiana verna

FIGURE 32 Map of vegetation in quadrat 1·1 - Gentiana verna (July 1970)

KEY to main species : · Sesleria caerulea, / Festuca ovina, N Gentiana verna,

T Thymus drucei, E Potentilla erecta, S Plantago maritima,

G Galium sterneri, H Prunella vulgaris



the quadrats were first established. This is clearly shown by the curves in Figure 33, where the values for the total populations recorded in each quadrat are plotted on a logarithmic scale and shown by a single line. These values include the survivors from the original population plus all new vegetative shoots.

Relatively little change was observed in the total populations of quadrats 1.1 and 7.2 whereas in quadrat 8.3 a large increase in 1970 was followed by a decrease in 1971 and 1972 such that the number of individuals recorded in the Autumn of 1972 was virtually the same as the number in the original quadrat population. In contrast increases of 30%, 36% and 50% in the original populations were recorded in quadrats 4.1, 8B.1 and Cronkley Fell, 10.1, respectively. These increases have resulted partially from the large recruitment of shoots in 1970 and their subsequent survival. This is shown by the increase in the total population between Autumn 1969 and Autumn 1970 (Figure 33).

Despite the large increases in the total number of individuals in some of the permanent quadrats, one of the features of the curves is their relative stability. With the exception of quadrat 8.3 the change in the number of individuals recorded at each visit was quite small by comparison with the number of individuals present at the previous visit. (The approximate date of each recording of the presence of vegetative rosettes can be seen along the bottom of the graph).

Maintenance of this apparently stable situation was achieved despite the rapid decline in the number of individuals recorded in the original quadrat populations. This decline is shown by the survivorship curves of the original recorded mixed-age populations (Figure 34) as well as by the curves for the groups of new vegetative shoots (Figure 35) appearing in the quadrats at each date of recording.

Half-life values based on the decay of the originally recorded mixed-age population in each quadrat give an indication of the rate of turnover in the number of individuals in the populations in Upper Teesdale. The figures shown in Table a vary between sites and suggest that complete replacement of the population could take place in as little as six years. This is in sharp contrast to half-life values obtained for some other perennial species, recalculated from data published by Tamm (1956b). For *Sanicula europaea* and *Filipendula vulgaris* values of > 50 years and about 18.4 years respectively were obtained (Harper 1967).

Losses of individuals from the quadrats were of two kinds: (a) when dead or dying rosettes were observed and at the next visit were not present, the plant was assumed to have died from natural causes, (b) when apparently healthy plants disappeared between concurrent recordings, these may have died or been removed (for example, by grazing). Some plants were pulled out by sheep, as rosettes bearing teeth marks have been observed.

On grazed areas of Widdybank Fell sheep may be important in determining mortality in this species. Of 376 individual rosettes lost over the four year period only one third had been recorded as being dead or dying. In contrast, of 33 individual plants lost from

Table a

HALF-LIFE VALUES

<u>Gentiana verna</u>

Quadrat	Half-life (years)	No.
1.1	3.0	76
4.1	4.7	127
7.2	4.1	57
8.3	2.8	29
8B.1	3.8	34
10.1	5.6	41

No. - Number of individuals in the originally recorded mixed-age population

the quadrat in the exclosure on Cronkley Fell, three quarters were recorded as being dead or dying.

This comparison indicates that sheep may have been responsible for the removal of a fairly high proportion of Gentiana verna rosettes. This fact is borne out by the half-life values in Table a, where it can be seen that the lowest figure was obtained for the individuals in quadrat 8.3 which was situated adjacent to a sheep track. The highest half-life value was obtained for the individuals in the quadrat on Cronkley Fell which was not grazed. However, it should be noted that this last figure was based on the decay in the number of individuals over 1971 and 1972 when, in general, mortality was low.

SECTION 4: SEASONAL SURVIVAL AND ANNUAL RECRUITMENT

There are some differences both between the seasons and between the quadrats in the seasonal survival rates for the quadrat populations (Table b). The lowest between season survival rates were recorded in the Summer of 1969 and over the Winter period 1969/70, and there is no significant difference at the one per cent level of probability between these figures. However, both values are significantly different at this level from all but one of the other overall seasonal rates. The exception occurs when a comparison is made between the survival rate over the Winter period 1969/70 and Summer 1970, although the difference is significant at the two per cent level of probability. (No data are available in some of the seasons for certain quadrats, either because they had not been established, as on Cronkley Fell, or because records were only obtained at the beginning and end of a twelve month period, quadrats 8.3 and 8B.1).

The differences between the quadrats were much less marked, although the survival rate of the individuals in quadrat 4.1 was significantly greater at the one per cent level of probability than the values obtained for the individuals in quadrats 1.1 and 7.2. Quadrat 1.1 had a significantly lower rate of survival for the individuals at the one per cent level than quadrats 4.1, 8B.1 and Cronkley Fell. No other comparisons between the quadrats are statistically significantly different.

The fact that the differences in survival rate are greater when comparisons are made between the seasons rather than between the quadrats suggest that climatic conditions may be important in determining the mortality of some individuals. The lower survival rates recorded for the seasons Summer 1969 and Winter 1969/70 could be related to low Winter temperatures of 1968/69 and 1969/70. In both these seasons the mean monthly temperature fell below freezing in several months (Figure 1). This may have been particularly important in 1969 when February and March were very cold, the low temperatures perhaps restricted growth at a critical time and increased the risk of mortality later in the plants' development.

Although between the quadrats the survival rates show smaller differences than between the seasons, the results indicate that grazing may be of some importance in determining mortality. The overall survival rate was greater for the individuals in the quadrat on Cronkley Fell and in quadrat 4.1. This to some extent bears out the conclusion reached in the previous section that mortality is greater on the grazed areas of Widdybank Fell. The fact that the value for

Table b

SEASONAL SURVIVAL

Gentiana verna

SEASON	QUADRAT 1.1	4.1	7.2	8.2	8B.1	10.1	
Winter 1968/69	0.86	0.87	0.95	-	-	-	0.89 ± 0.02
Summer 1969	0.63	0.85	0.59	0.66	0.74	-	0.70 ± 0.03
Winter 1969/70	0.54	0.88	0.82		0.77	-	0.75 ± 0.02
Summer 1970	0.81	0.88	0.80	0.83	0.82	0.85	0.83 ± 0.02
Winter 1970/71	0.78	0.91	0.83	0.80	0.91	0.92	0.86 ± 0.02
Summer 1971	0.83	0.79	0.91	0.74	0.87	0.82	0.83 ± 0.02
Winter 1971/72	0.83	0.92	0.85	0.84	0.88	0.88	0.87 ± 0.02
Summer 1972	0.86	0.87	0.73	0.83	0.87	0.87	0.84 ± 0.02
	0.77 ± 0.02	0.87 ± 0.01	0.81 ± 0.02	0.81 ± 0.03	0.84 ± 0.02	0.87 ± 0.02	

Overall seasonal survival for each quadrat population both between quadrat and between season is shown ± standard error

quadrat 4.1 is equal to that for the individuals in the quadrat on Cronkley Fell is difficult to explain, as this area had the appearance of being heavily grazed. However, all the other quadrat values are lower than that obtained for the quadrat population on Cronkley Fell.

Annual recruitment rates vary a great deal both between the quadrats and between the years. The rates given in Table c are expressed per individual present in the quadrats in the Summer of each year. The largest difference is seen when comparisons are made between the figures for the four years, when twice as many new individuals appeared in 1970 as in the other years.

Differences between the quadrats were less marked. However, they are still considerable and the rate of recruitment of individuals in quadrat 8.3 was the highest at 0.73 per individual. To some extent the quadrats with the lower recruitment rates were those with lower rates of mortality. Thus the two quadrats with highest survival rates (lowest mortality), Cronkley Fell and quadrat 4.1, were also the quadrats with the lowest rates of recruitment. Correspondingly the quadrats with the lowest survival rates (highest mortality) had the highest recruitment rates. These results suggest that the populations were self regulatory in that the higher the rate of mortality of individuals, the greater the rate of recruitment.

SECTION 5: AGE-SPECIFIC SURVIVAL AND AGE DISTRIBUTION

Survival of individuals of known age was remarkably similar for groups of individuals appearing in the quadrats at different times

Table c

ANNUAL RECRUITMENT

Gentiana verna

	QUADRAT						
YEAR	1.1	4.1	7.2	8.3	8B.1	10.1	
1969	0.38	0.43	0.50	-	0.41	-	0.43*
1970	2.10	0.63	0.91	1.94	0.74	0.54	0.98*
1971	0.65	0.33	0.31	0.69	0.49	0.34	0.43*
1972	0.28	0.32	0.49	0.23	0.26	0.50	0.34*
	0.66*	0.42*	0.53*	0.73*	0.45*	0.45*	

Figures shown with an asterisk represent the annual recruitment rates for the summed totals of each quadrat and year

(Figure 35). There is no indication that there was any increased risk of mortality in the early stages of the rosettes' life and all the curves are approximately linear. The linear nature of the curves (also shown in the curves from the originally recorded mixed-age populations) indicates that there was a constant risk of mortality throughout the life of the individual plant. The curves conform to Deevey (1947) type 2, and are exponential in form.

The curves have very similar slopes indicating that not only was mortality independent of the age of the individual but that age cohorts had similar rates of decay. There is superimposed on these curves a small seasonal variation which indicates that the rate of loss of individuals from the quadrats was slightly greater during the growing season. This conclusion bears out the suggestion made by Kay and Harper (1974) that density stresses in the sward are responsible for controlling death rates and that these stresses are at their most intense during the period of active growth.

The majority of individuals present in all the quadrats in the Autumn of 1972 were new vegetative shoots which had appeared during the study period (see Table d, where the distribution of the different age-groups is shown for each quadrat). Clearly the least important age-group as far as the actual number of individuals is concerned was the group which was three to four years old. The relatively small proportion of individuals in this age group was due mainly to the fact that the recruitment rate in that year was small. Although the recruitment rates of individuals in 1971 and 1972 were also low, because of their more recent origin and relatively low mortality, they form a fairly high proportion of the population.

Table d

AGE-DISTRIBUTION IN AUTUMN 1972

Gentiana verna

	AGE IN YEARS	QUADRAT 1.1	4.1	7.2	8.3	8B.1	10.1
Present Autumn 1968	>4	9	33	12	-	-	-
'Born' year Aut. 1968-Aut. 1969	3-4	4	24	1	4*	8*	-
'Born' year Aut. 1969-Aut. 1970	2-3	27	45	13	11	11	20** (11)
'Born' year Aut. 1970-Aut. 1971	1-2	25	30	11	15	15	11
'Born' year Aut. 1971-Aut. 1972	<1	17	42	20	8	15	23

* Individuals > $3\frac{1}{2}$ years old, first recorded Spring 1969

** Individuals > $2\frac{1}{2}$ years old, first recorded Spring 1970

The figure in brackets represents the number of individuals appearing in quadrat 10.1 in 1970 and surviving to Autumn 1972

Plants were able to flower in their second year and therefore all age groups except those 'born' in 1972 were of potential importance for seed production. This distinction is perhaps not of particular importance as very few fruits reach maturity on grazed areas of Widdybank and Cronkley Fells and as yet no seedlings have been observed.

SECTION 6: REPRODUCTIVE PERFORMANCE

Sexual reproduction was not important in the short-term for the maintenance of the populations of Gentiana verna growing under natural conditions on Widdybank and Cronkley Fells. However, the data so far collected in this study indicate that the species has a very high reproductive potential*. Table e shows that overall approximately 7% of the individual rosettes produced flowers in any one year. Usually only one flower was produced per rosette and in the permanent quadrats and sample areas no ripe capsules were observed.

Production of flowers varied both between the sites and between the years, with the greater differences occurring between sites. The lowest value of 2% flowering was obtained for the individuals growing at site 8, which was crossed by a sheep track. The highest value at site 8B may have been related to the presence of Calluna vulgaris which could have protected the plants from the ravages of sheep, or provided some protection from the harsh climate. Conclusions are, however, very difficult because, of the other sites, Cronkley Fell was ungrazed, site 4 also had Calluna vulgaris and neither produced particularly high proportions of flowering plants.

---

* Measured in terms of the production of potential new plants (seeds) See Section 8.

Table e

ANNUAL FLOWER PRODUCTION - BETWEEN SITES

Gentiana verna

SITE	Total No. Individuals	No. Flowering	Percentage Flowering
1	884	100	11
4	922	46	5
7	520	26	5
8	447	11	2
8B	506	70	14
10	280	24	9

Differences between years were much less marked, with 1969 being the most prolific as far as the production of flowers was concerned, (Table f).

The effects of predation by animals on the ability of plants to produce ripe capsules is clearly shown by comparing the number of flowers which develop to produce ripe capsules on grazed and ungrazed areas on both Fells. In 1970, of 14 marked flowering plants in the exclosure on Cronkley Fell, 7 produced ripe fruits with apparently viable seed. In an experimental exclosure on Widdybank Fell in the same year 14 ripe capsules were produced. This is in sharp contrast to the single capsule, which did not reach maturity, produced from 67 marked flowering individuals on grazed areas of Widdybank Fell.

In 1972 on grazed areas of Widdybank Fell of 64 marked flowering individuals none produced ripe capsules. However, in the sheep-proof exclosure on the Fell, 105 ripe capsules were produced in the same year.

Fruits collected from inside the exclosures showed that a very large number of seeds can be produced (see Section 7, Table g). Assuming that all the flowers that were produced went on to form fruits, the potential for reproduction would be very high with approximately 1,183 seeds produced per 100 individuals in the population. Although no ripe fruits were observed in any of the permanent quadrats or sample areas, each year one or two ripe capsules were found on Widdybank Fell. These may be very important for the long-term survival of the species, allowing genetic adaptation to environmental change.

Table f

ANNUAL FLOWER PRODUCTION - BETWEEN YEARS

Gentiana verna

YEAR	Total No. Individuals	No. Flowering	Percentage Flowering
1969	728	77	11
1970	883	73	8
1971	1,030	57	6
1972	918	70	8

SECTION 7: SPECIES BIOLOGY

The small short-lived perennial herb usually produces one flower and in any one year approximately 7% of the rosettes present in the permanent quadrats and sample sites flowered. The rosettes which flowered usually died without flowering again. This can be seen in Figures 36 and 37 where the behaviour of the individuals in three of the six permanent quadrats is shown. Of 93 flowering rosettes recorded in all the permanent quadrats only 8 flowered twice. Two of these individuals, one of which flowered in 1969 and 1970, and the other in 1969 and 1972, were still alive in the Autumn of 1972. Thirty flowering rosettes died within one year of flowering and a further 19 died within two years. Thirty of the 93 rosettes were still alive in the Autumn 1972 although 22 of these had flowered in that year.

Individuals were able to flower in their first year, although of all the new vegetative shoots only few did so. More frequently flowering took place in the second or third year (Figures 36 and 37).

Viable seed can be set in Upper Teesdale and ripe capsules have been found in exclosures on both Widdybank and Cronkley Fells. As already noted very few capsules are produced on grazed areas of the two Fells because of predation, particularly by sheep. However, other factors may be important, such as insects which often bite through the calyx and corolla to obtain nectar and perhaps damage the flower or fail to bring about pollination. Wind and heavy rain may also play a part by damaging immature capsules.

The main flowering period in Britain as a whole is from the end of April and throughout May (Elkington 1963). In Teesdale, on the upper parts of Widdybank Fell, flowering in 1969, 1971 and 1972 occurred at this time, but in 1970 in response to a late Spring, flowering did not start until late May, finishing in late June.

Occasional flowers in the Autumn are not unusual. Flowers were observed in October in 1968, 1970 and 1971, and one plant in flower on Widdybank Fell in December 1970 may have been stimulated by a very short cold spell in early November. (Buds are initiated in the Autumn of each year). Plants transferred from Teesdale to Durham in 1970 flowered in 1971 and 1972 some 7 days earlier than plants growing under natural conditions in Teesdale. In 1971 several plants flowered in the first week of October.

In both 1971 and 1972 on several fine, still days individuals of <u>Bombus lucorum</u> were seen to be active on flowers of <u>Gentiana verna</u>. Examination of many flowers showed that all had had the calyx and corolla bitten through. Further details of floral biology and other species characteristics can be found in the Biological Flora account by Elkington (1963).

Seed production per capsule is shown in Table g, and was obtained from capsules collected within the exclosures. Elkington quotes figures of 379 ± 20 seeds per capsule for a sample of 25 capsules from Ballyvaughan, Co. Clare. Five capsules from a population in Teesdale gave a mean number of 113 ± 20, a figure which compares favourably with the values obtained during the course of this study.

Table g

SEED PRODUCTION

Gentiana verna

YEAR	Widdybank Fell	Cronkley Fell	Durham
1970	143 ± 11	182 ± 30	None
1971	132 ± 13	None	60 ± 8
1972	182 ± 11	None	131 ± 18

Figures for seed production are expressed as a mean per capsule ± standard error

The very low figure obtained for individual plants transplanted to tubs at the University of Durham in 1970 and flowering in 1971 may be due to the disturbance of the plants. This is to some extent borne out by the figure for the mean number of seeds produced per capsule in 1972 which was more than twice the value obtained in 1971.

SECTION 8: LIFE STRATEGY

Gentiana verna is a ~~relatively~~ short-lived perennial, whose effective reproduction is by means of fine underground stolons which terminate in a rosette of leaves. Sexual reproduction does occur and may be important in the long term survival and evolution of the species. However, as has been noted, few ripe capsules are produced and so far no seedlings have been observed on either of the Fells.

Despite this fact and the relatively high rate of annual mortality of 30 per cent of all shoots present in the quadrats, the total populations remained fairly stable throughout the study period. Indeed in three of the permanent quadrats increases of between 30 and 50 per cent were recorded between the dates the quadrats were first recorded and Autumn 1972.

Replacement of the population by means of the production of new vegetative shoots is a continuous process throughout the growing season. The annual rate of recruitment of these new shoots to each of the quadrat populations exceeds the rate of loss of individuals. The value of 37 new shoots per 100 plants in the population is reflected by the overall increases observed in the total quadrat populations.

A fairly high proportion of the additional rosettes appeared in 1970 when the climatic conditions were probably most favourable to plant growth (see Chapter two, Figure 1).

Mortality of these new shoots, as with mature individuals, was independent of the age of the plant. Although there is no evidence to suggest that flowering increases the risk of a plant dying, rosettes seldom flowered a second time. There is some indication that mortality may be affected by grazing intensity. The half-life values in Table a do to some extent correlate with apparent grazing pressures, the lowest half-life value being obtained for the quadrat at site 8, which was situated on a sheep track.

Survival rates discussed in Section 4, whilst helping to confirm the conclusions about the effect of grazing, do suggest that climatic factors may also have been important in determining mortality. In this context the higher survival rates for the Winter seasons suggest that stresses imposed both by the growth of the plant and of the surrounding vegetation during the growing season were sufficient to increase the risk of mortality. This conclusion to some extent bears out the findings of Langer et al. (1964) who, over a period of 3 years, recorded the rate of loss of genetic individuals in populations of Phleum pratense and Festuca pratensis. They found the rate of mortality was greatest at the peak of the growing season, March to June, whilst there was a negligible loss during the Winter months.

The reproductive potential of this species is high. An estimate of the maximum possible number of seeds which would be produced annually if all the flowers went on to produce ripe fruits shows that some

1,183 potential plants could be formed per 100 plants present in the population. This figure gives some indication of the devastating effect which grazing and perhaps to a lesser extent other factors have on the potential of the population to produce new individuals by sexual reproduction.

The results clearly indicate that vegetative reproduction alone was able to maintain the populations of <u>Gentiana verna</u> on Widdybank and Cronkley Fells in the short term, at least. This was despite the very high rates of mortality which were recorded in the quadrat populations.

It is possible that the plants in Teesdale, which differ morphologically in both calyx and leaf character from those growing in the Burren area of Co. Clare (Elkington 1972), have originated from a relatively small number of individuals developing from seed. Reproduction by vegetative means from those plants has thus given rise to extensive clones, with individuals morphologically similar.

To what extent this sexual reproduction would be important in the replenishment of the population under natural conditions, if grazing were eliminated or reduced, is not known. Continued study of the quadrat on Cronkley Fell, or even in the Burren where grazing is much less intense than the area studied in Upper Teesdale, should help answer this question. The long term survival of this species may depend on the occasional plants arising from seed and allowing genetic selection to occur.

Figure 33

TOTAL POPULATION

Gentiana verna

FIGURE 33

TOTAL POPULATION-*Gentiana verna*

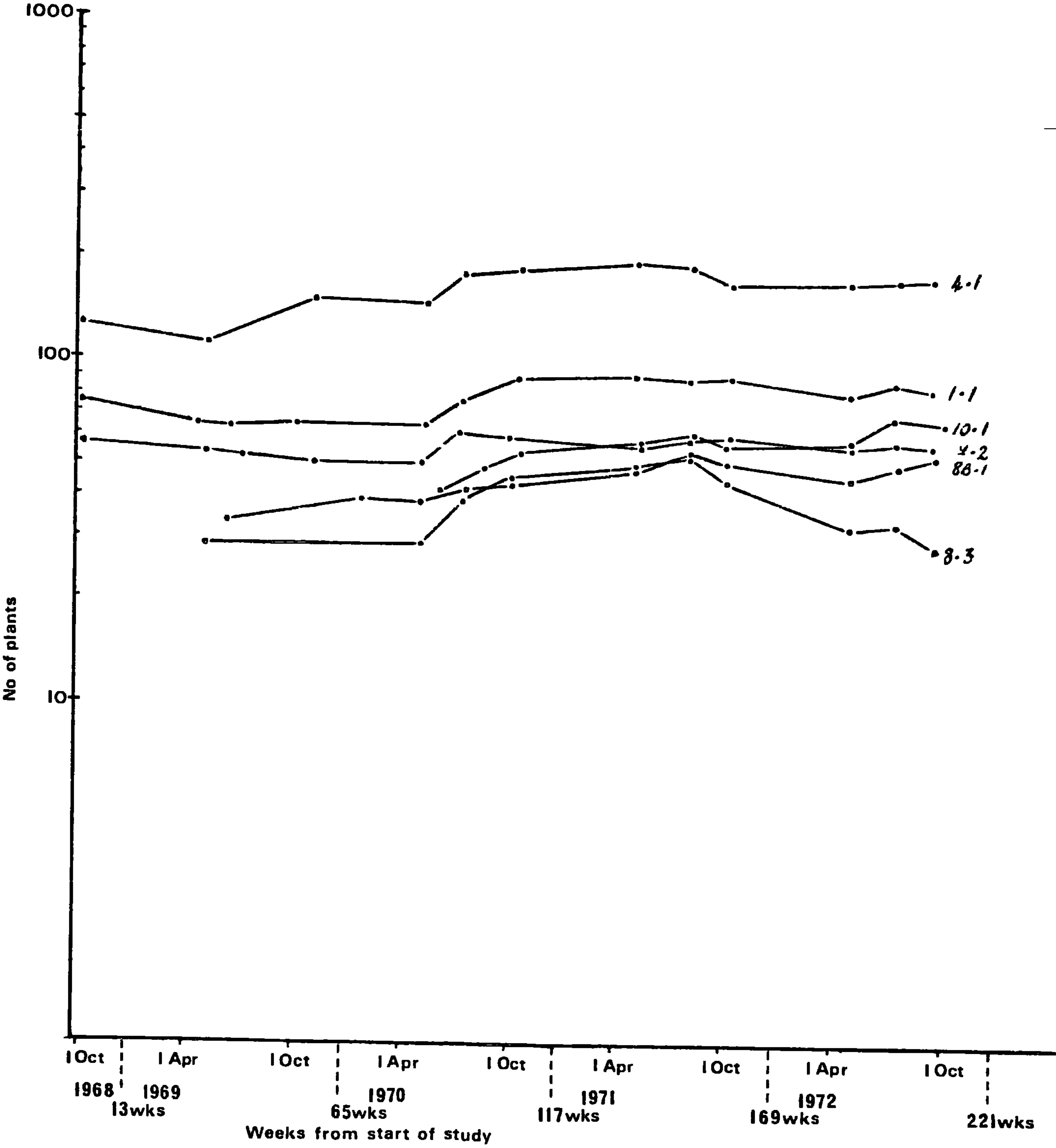


Figure 34

SURVIVORSHIP CURVES OF MIXED-AGE POPULATION

Gentiana verna

FIGURE 34

SURVIVORSHIP curves mixed-age populations – Gentiana verna

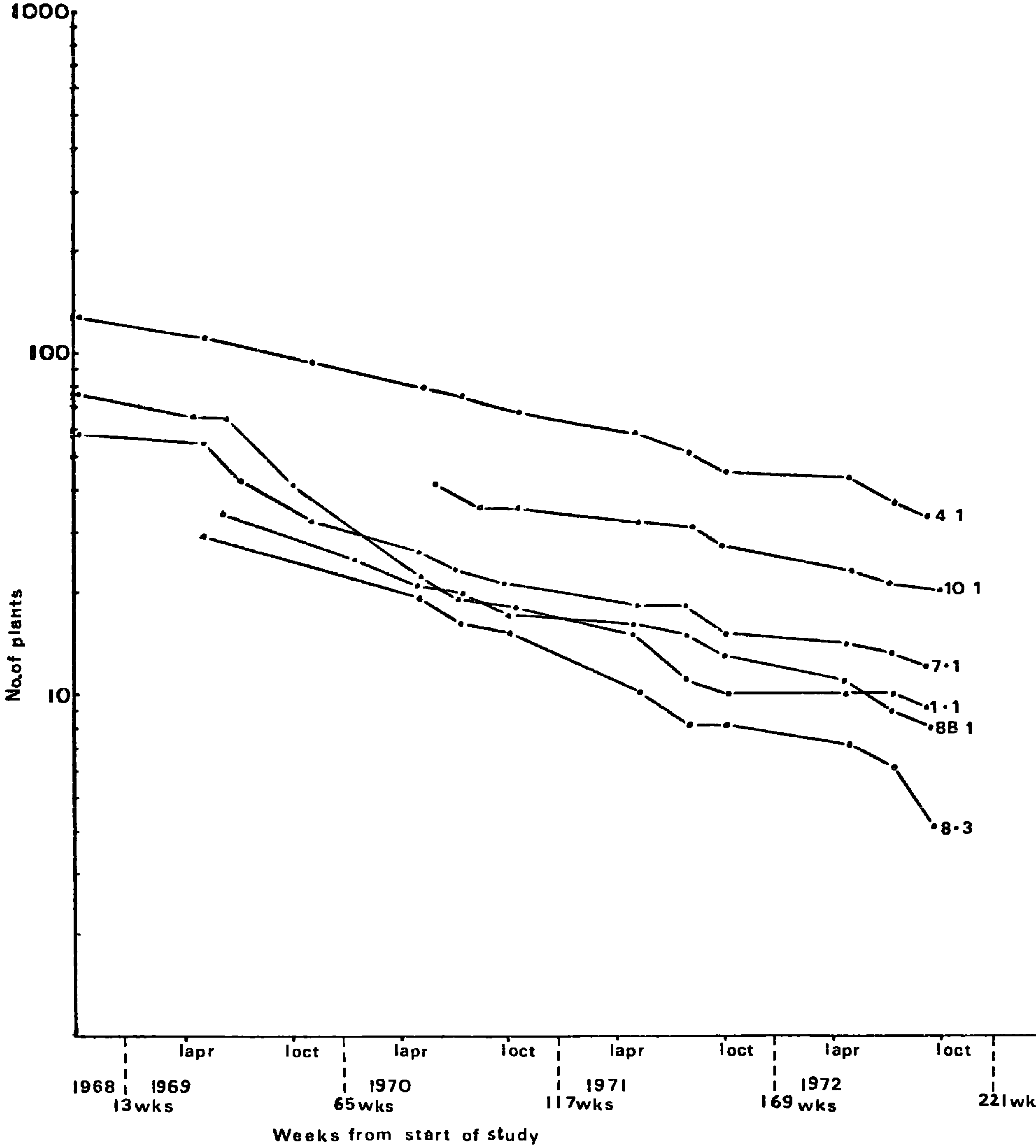


Figure 35

SURVIVORSHIP CURVES OF VEGETATIVE
SHOOTS 'BORN' AT THE SAME TIME

Gentiana verna

FIGURE 35

SURVIVORSHIP curves of vegetative shoots "born" at the same time –

Gentiana verna

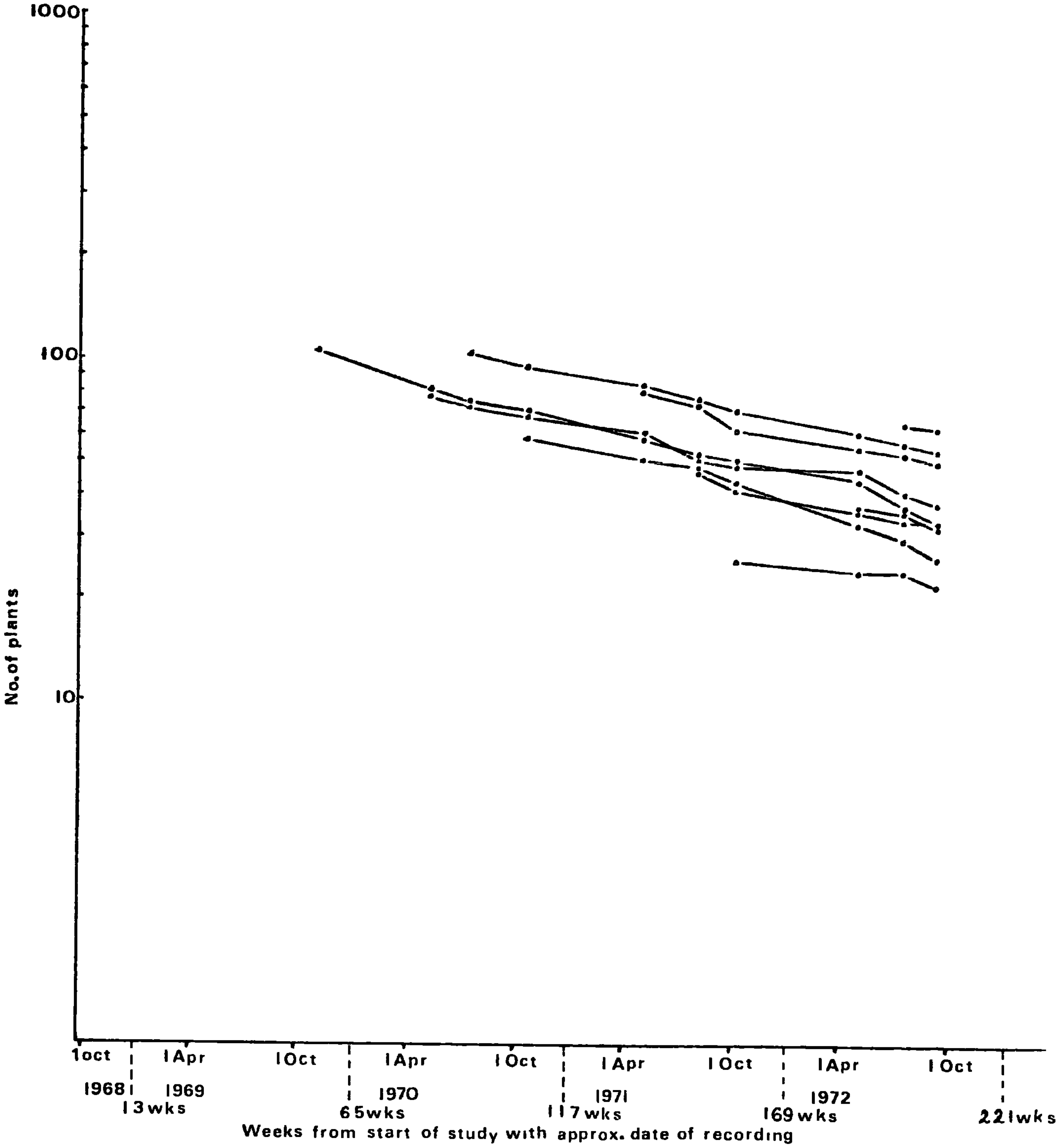
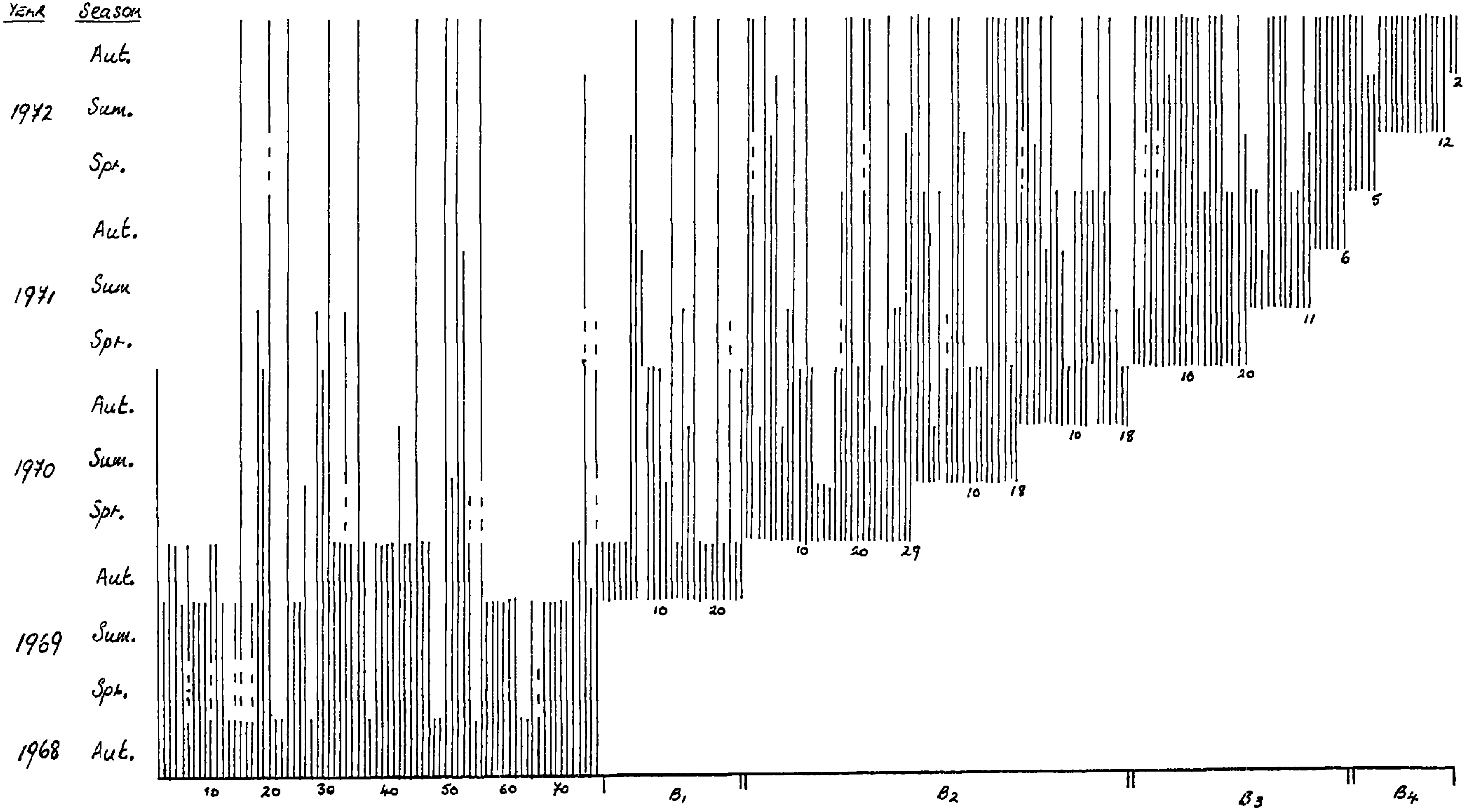


Figure 36

BEHAVIOUR OF INDIVIDUALS IN QUADRAT 1.1

Gentiana verna

FIGURE 36 Behaviour of individuals in quadrat 1·1 - <u>Gentiana verna</u>



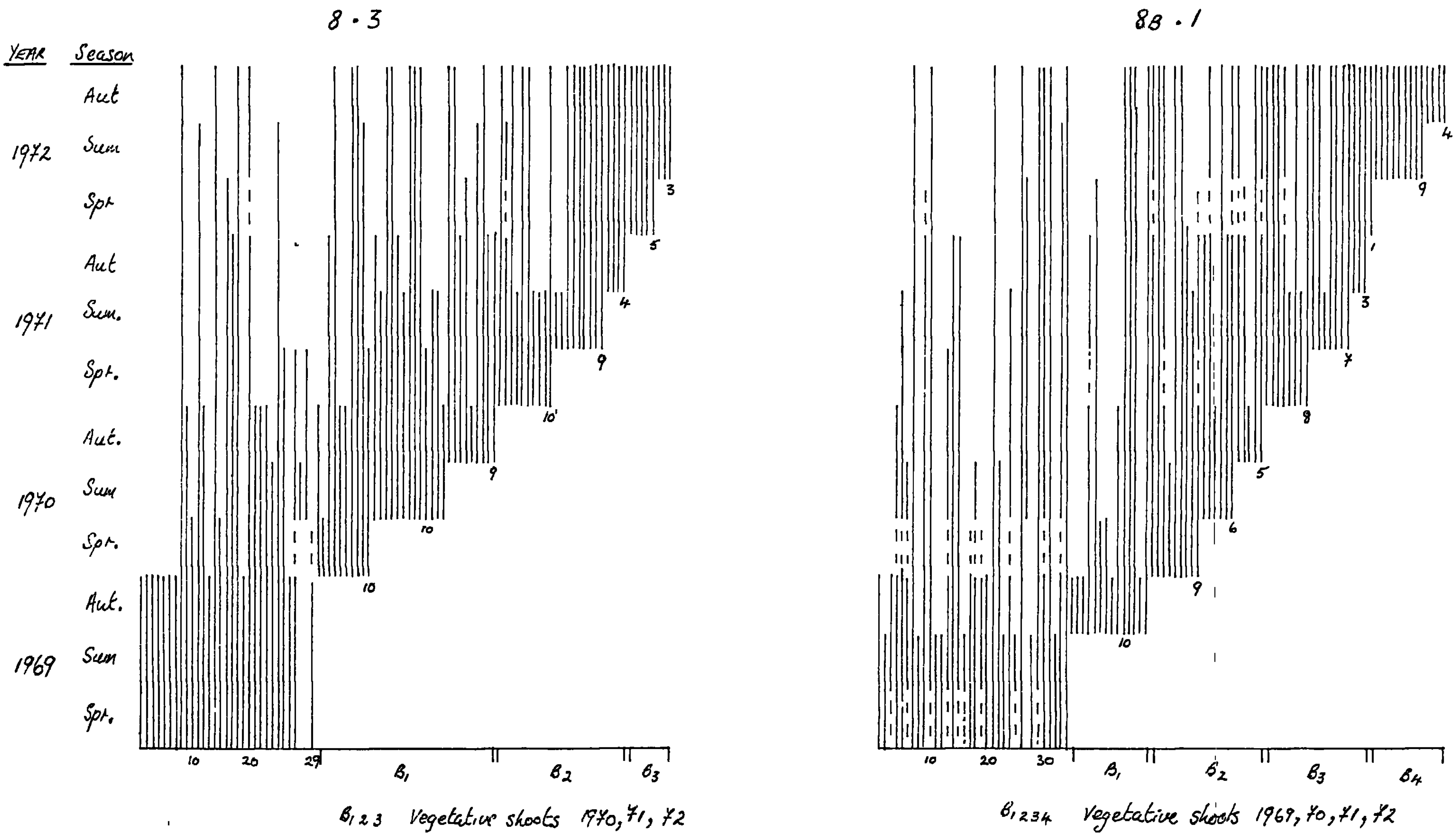
B1234 Vegetative shoots 1969, 70, 71, 72

Figure 37

BEHAVIOUR OF INDIVIDUALS IN
QUADRATS 8.3 AND 8B.1

Gentiana verna

FIGURE 37 Behaviour of individuals in quadrats 8·3 and 8B·1 - Gentiana verna



CHAPTER TEN

COMPARISON OF LIFE-STRATEGIES

The survival of any plant species depends on the ability of the population to replace individuals by vegetative growth and sexual or apomictic reproduction. The particular life-strategy of each species is adapted so as to overcome environmental constraints which tend to limit or reduce the size of the population. The pattern of growth in a potentially explosive population is often expressed by the logistic equation, Harper (1967):

$$\frac{dN}{dt} = r\,N\,\left(\frac{K - N}{K}\right)$$

Rate of growth of population = intrinsic rate of natural increase x degree of realization of the potential increase

K represents the carrying capacity of the habitat;

N represents population size.

In plant populations the intrinsic rate of natural increase 'r' has, in effect, two values; one associated with seed output, the other with vegetative reproduction. The value for the first of these is usually, although not always, high and is '. . . associated not only with high risk but also with spread of the risk over a large number of small capital investments (or bets!)', Harper (1967).

Most plant species whether annuals, biennials or perennials produce seeds. (Note that in Teesdale some perennials such as Viola rupestris x riviniana produce flowers which are sterile). Some species may produce very large numbers of seed and are often annuals or biennials which inhabit open or unstable habitats. The value of seed output can be as high as 2×10^4 seeds per plant for species which grow in these situations, Salisbury (1942). The strategy of these species is essentially that of the opportunist: by producing large numbers of small, light seed which can often be transported over great distances, advantage can be taken of uncolonised, open situations which may have been newly-created.

Seed production in perennials is usually quite low by comparison if the annual rate per shoot is measured. However, when the rate of seed production is measured for a clone over its life-time, or even the individual (unit of reproduction) which may produce seeds in successive years, the actual seed output may be very high. It is interesting in this context to compare Polygala amarella and Draba incana, which are both perennial species relying entirely on seed production for the maintenance of the population. The former species produces small numbers of large seeds over several years,whilst the latter species produces large numbers of small seeds and then dies (see below).

Perennial herbs particularly those growing under grazed conditions must often rely on vegetative reproduction for the maintenance of the population. This mode of reproduction represents a second value of 'r' which Harper (1967) considers is often lower than the value for seed output and '. . . is often associated with heavy and continuous capital investment, a "cautious" policy of placing the investments and low risk'.

Clearly, the method of reproduction is only part of the life-strategy of any species. The rate of mortality at each stage in the life-cycle, the time taken for plants to mature to an age where they are able to make a contribution to population maintenance and the actual rates of recruitment, are all important in determining the survival of the species. The species included in this study have a variety of life-strategies, ranging from *Linum catharticum* which in Teesdale is a biennial, to *Viola rupestris x riviniana* which is a perennial reproducing entirely by means of the production of vegetative shoots.

The strategy of each of the species is best appreciated by making reference to the diagrams showing the behaviour of some of the quadrat populations for each of the species (after Tamm, 1948), Chapters four to nine. Of the two species not included in these six chapters, *Linum catharticum* is a biennial and *Carex ericetorum* is a perennial which reproduces by the production of vegetative shoots. (The behaviour of the individuals in one of the two permanent quadrats recorded for *Carex ericetorum*, quadrat 8.1, is shown in Figure 38).

In *Linum catharticum* seed germinates in the Spring and develops into a small plant with six to eight leaves which survives through the Winter. The typical fairy flax plant develops in the following Spring and Summer, flowering and setting seed in late Summer, after which the plant dies.

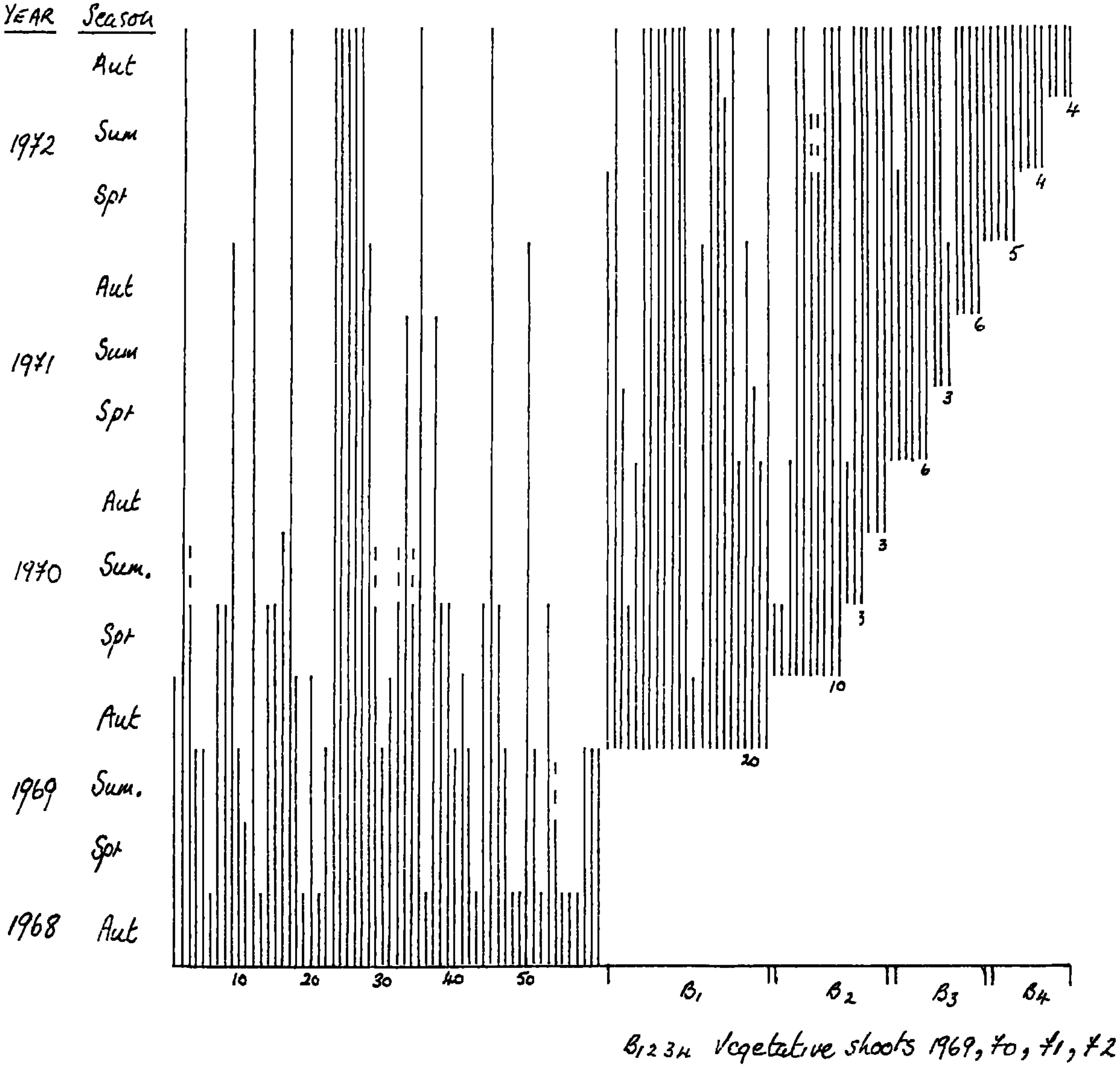
All the other species are perennial herbs which reproduce by the production of vegetative shoots or seeds, or both.

Figure 38

BEHAVIOUR OF INDIVIDUALS IN QUADRAT 8.1

Carex ericetorum

FIGURE 38 Behaviour of individuals in quadrat 8 1 - *Carex ericetorum*



Some of the parameters used to describe the behaviour of the species studied on Widdybank and Cronkley Fells are given in Table a. The figures for each species in rows a-h represent the overall values for the populations based on data from the permanent quadrats. The figures in rows i-l give an indication of the overall reproductive performance of each species based on data obtained from both permanent quadrats and sample sites. (These figures have been used in estimating the annual seed production per 100 plants, row g).

Gentiana verna (Chapter nine) and Carex ericetorum reproduce by means of the production of new vegetative shoots, the former from long underground stolons, the latter from an underground stem. Both species are able to produce seeds, although Gentiana verna seldom does so under grazed conditions because the flowers are removed by sheep. A number of seeds are produced by Carex ericetorum, although some inflorescences are removed as a result of predation by sheep. However, no seedlings of either species were observed during this study.

The behaviour of the quadrat populations for Gentiana verna (Figures 36 and 37) and Carex ericetorum (Figure 38) may be the behaviour of the individuals of a single clone (the sub-population of Harper and White, 1974). The age of the clone cannot be determined, although the fact that no seedlings have been observed suggests that they could be very old. The estimates of clonal longevity for Festuca rubra, Festuca ovina and Trifolium repens, Harberd (1961), (1962) and (1963) respectively, suggest that for these species, their age should be measured in centuries.

This is in sharp contrast to the length of life of the individual vegetative shoots of Gentiana verna and Carex ericetorum which has a maximum value of approximately eight years. This figure is based on the half-life values given in row h, and taken together with the rate of annual mortality of all plants, row c, shows that the rate of loss of individuals for these species is high.

Other studies in the pattern of change of shoots derived from a single seedling are very few. Langer (1956), showed that tillers of Phleum pratense had a very limited life-span which was normally not greater than one year. The life-span of Ranunculus repens was found to be of the same order as for Gentiana verna and Carex ericetorum, Sarukhan and Harper (1973). For Ranunculus repens the maximum life-span was approximately six years for the individuals known to have arisen as a result of vegetative reproduction. Seed was produced but appeared to be unimportant to the maintenance of the population.

By contrast, Tamm's study of several perennial herbs in meadow and forest plots indicates that the rate of population change of established plants may be very slow, Tamm (1948) and (1956b). For the species studied, which included Primula veris and Anemone hepatica the annual rate of loss of plants ranged from 0% to 11%.

Despite the fact that for both Gentiana verna and Carex ericetorum, almost one third of the plants in the population were lost annually, the total number of shoots changed little between Autumn 1968 and Autumn 1972 and for Gentiana verna showed an increase. This was brought about by a rate of recruitment of new vegetative shoots, row d, which more than compensated for the loss.

It is clear that these species are able to survive by the production of vegetative shoots. However, both are capable of producing seed which may be important to the long term survival of the species by allowing genetic variation, and therefore possible adaptation of the population to changing environmental factors.

Reference to rows i-l will show that for these species, less than 10% of the population actually flower. In the case of Gentiana verna, usually only one flower is produced per plant. However, just one ripe capsule can produce a large number of small seeds. Overall, this results in a potential rate of seed production (assuming all flowering plants produce ripe capsules) of 1,183 seeds per 100 plants in the population. This compares with a figure of 26 for Carex ericetorum where a small number of large seeds are produced per flowering plant.

Carex ericetorum thus relies on a cautious policy of capital investment in seed, similar to that for vegetative reproduction. Presumably, the production of a smaller number of large seeds is associated with a lower risk of mortality at the stage of seedling establishment. Unfortunately, as no seedlings have been observed it is not possible to determine whether this is so. The two values of r (the intrinsic rate of natural increase) are for this species approximately the same. Gentiana verna, on the other hand, has two very different values: a low value for the cautious policy of capital investment attached to vegetative reproduction, and a much higher value for seed production. Presumably, this second value is associated with a high risk of mortality.

Since so few capsules of Gentiana verna have been observed on the Fell it is difficult to determine the precise significance of this high value of seed production. However, it is possible that it represents a strategy which allows new genotypes to become established in open conditions. This could have been very important during the whole of the late and post-glacial periods especially the forest maximum, when suitable habitats were at a premium. This method of reproduction would enable the species to colonise any new open or semi-open sites.

Viola rupestris x riviniana also maintains its population in Upper Teesdale by the production of new rosettes by vegetative growth. Unlike Carex ericetorum and Gentiana verna seed cannot be produced by flowering rosettes because the flowers are sterile. Figures 18 and 19, Chapter six, show the behaviour of vegetative shoots derived from established plants of the hybrid. As already indicated in Chapter six, these new hybrid plants arise very infrequently and the figures may each show the behaviour of a clone. (It is possible that the seeds produced in one capsule following successful cross pollination between the parents, may have germinated in the same area. Therefore, if several of these seedlings became established, there may in fact, be several clones of the same age close to one another).

The age of the clones are impossible to determine, but the area covered by some of the groups of plants indicate that they may be very old. The half-life value (row h), based on the decay of the original populations of Viola rupestris x riviniana, indicate that individual rosettes might be expected to live for 28 years or longer. This figure taken in conjunction with the annual rate of mortality of the rosettes, shows that change in the population is a fairly dynamic process, but that the rate of loss is less than half that for Carex ericetorum and Gentiana verna.

The lower rate of turnover is paralleled by the lower rate of recruitment of new vegetative rosettes which is again half that obtained for the other two species. This lower recruitment was, however, greater than the annual rate of loss, and there was a gradual increase in the population over the period of recording. Clearly, this hybrid represents a genotype which is successful in its reproductive strategy under present environmental conditions.

Viola rupestris and Viola riviniana maintain their populations on Widdybank Fell both by the production of vegetative shoots and seedlings. The behaviour of the individuals in the two populations is shown in Chapter four, Figures 7, 8 and 9, for Viola rupestris, and Chapter five, Figures 13 and 14, for Viola riviniana. As new individuals arise both by the production of new shoots and by germination of seed and its establishment, the populations are made up of a mixture of the 'ramets' and 'genets', respectively, of Kay and Harper (1974).

The individuals in both these populations are relatively long-lived. The half-life values, based on the decay of the mixed-age population, indicate that rosettes of Viola rupestris may live for up to 18 years, and rosettes of Viola riviniana up to 24 years. Blake (1935) found that the life-span of prairie plants was similar, ranging from 10 to 20 years. As with Viola rupestris x riviniana the annual rate of mortality is approximately half that of Carex ericetorum and Gentiana verna. This slower rate of loss of individuals requires an equally slow rate of recruitment to maintain the population.

Recruitment of vegetative shoots in both species is higher than that for seedlings. Two thirds of all new individuals of Viola riviniana appeared as a result of vegetative reproduction. In Viola rupestris, where seedling recruitment attained a greater significance in open habitats, than in those which were more closed, almost half the new recruits were seedlings. These figures compare with those obtained by Sagar (1959) and (1970), for Plantago lanceolata, where 25% of the total number of new individuals appearing over a two-year period were produced from vegetative shoots, the remainder being seedlings.

The rate of recruitment of both vegetative shoots and seedlings when added together is far in excess of the number of plants which are lost. In fact, the annual rate of production of new vegetative shoots is greater than the rate of loss and theoretically could ensure the continued survival of the populations.

Seedling recruitment, however, provides a means whereby both species are able to colonise new areas. This could be extremely important to the long-term survival of Viola rupestris, in particular, which appears to be near the limit of its tolerance in the closed grass swards. The actual rate of seed production indicates that this mode of reproduction also involves a relatively high investment in a few large seeds. This cautious policy represents a low value of 'r' and is associated with low risk. (Although the figure for the annual rate of mortality of seedlings of Viola rupestris is high, it has been exaggerated by the large influx of seedlings. Only one other group of seedlings showed an increased rate of mortality during the early stages of establishment /Viola riviniana seedlings 1971/. For all the other groups the risk of mortality was the same throughout the life of the individual).

When compared with the rate of seed production for the other species, both species of violets produce slightly more seed than Carex ericetorum, but much less than Draba incana and Linum catharticum.

The relatively small contribution made by seed produced from open flowers can be seen by making reference to row k. The figures in brackets represent the mean number of fruits per flowering plant from open flowers. Cross pollination of these open flowers and the production of seeds provides a potentially outbreeding mechanism which allows the exchange of genetic information. This mechanism could be important to the long-term survival of both species of violet.

Once established, individuals of both species, whether from seed or vegetative shoots, take several years to develop to the flowering stage. Thereafter, they may flower in several successive years. Both species have an overall strategy of slow population turnover and slow recruitment, which involves a cautious policy of replacement by vegetative shoots and seedlings.

Draba incana and *Polygala amarella* both rely solely on the production of seed, its germination and the subsequent establishment of seedlings for the replenishment of their populations. The behaviour of the individuals in the populations of *Draba incana* and *Polygala amarella* is illustrated in Chapter three, Figures 30 and 31, for the former species and in Chapter seven, Figures 24 and 25, for the latter. The individuals, each represented by a line in the figures, appear initially as seedlings and are equivalent to the 'genets' of Kay and Harper (1974).

Although both reproducing by means of the production of seed, the two species have very different life strategies. *Draba incana* behaves as a mono-carpic perennial, a 'big bang' producer of Gadgil and Bessert (1970) as does *Linum catharticum*, whilst *Polygala amarella* is a repeating producer. In both species the rate of population turnover, of individuals greater than one year of age, is high. The figures in row e show that for *Polygala amarella* the annual rate of mortality is similar to that obtained for *Carex ericetorum* and *Gentiana verna* whilst that for *Draba incana* is higher.

Draba incana, a species found only in open conditions, relies on its ability to produce large numbers of small seeds, row g, which germinate producing a large number of seedlings, row e. Thus, this species has a high value of 'r', which is associated with high risk, both at the seed to seedling and seedling to young plant-stages. This is clearly illustrated by the figures for annual seed production, annual seedling recruitment and annual seedling mortality.

Polygala amarella has a rather different life-strategy, in this case producing smaller numbers of large seeds. Unlike *Draba incana*, the plant may flower in several successive years. In this way the species acts as a repeating producer. The rate of seed production represents a fairly low value of 'r', producing only twice as many seeds annually as plants that are lost. However, the rate of mortality of the seedlings is lower than that obtained for the plants over one year of age. Clearly, this low rate of seed production is associated with low risk, a cautious policy, similar to that of seed production in *Viola rupestris* and *Viola riviniana*.

These two different strategies reflect the different habitats in which the two species survive. *Draba incana* only occurs in open or disturbed ground, whilst *Polygala amarella* grows in Upper Teesdale in a closed vegetation. The first species is clearly an opportunist, and the second, by producing a relatively small number of large seeds, gives the emerging seedling a good chance of survival in a habitat where their establishment must be quite difficult.

For both species, the method of reproduction has resulted in an increase in the population over the period of recording. In the case of *Draba incana* this increase is 50% on the originally recorded mixed-age populations in the quadrats. It must be remembered that *Draba incana* produced large numbers of seed and many of the plants present at the end of the study period were still very small. New plants of each species take some time to develop to the stage when they are able to make a contribution to seed production.

In some respects, for instance the annual rate of seed production and annual mortality of seedlings, *Draba incana* and *Linum catharticum* are very similar. *Draba incana* appears to be, in fact, an extended biennial. It is possible that the cold and wet climate of Upper Teesdale slows down the development of its rosettes so that instead of being a biennial the species becomes a mono-carpic perennial.

Other perennial species which reproduce entirely by the production of seed include: *Ranunculus* ~~*acris*~~ bulbosus, Sarukhan (1974), *Trifolium pratense*, Rabotnov (1960) in Harper and White (1970) and *Anthoxanthum odoratum*, Antonovics (1972). *Trifolium pratense* is perhaps the most interesting of the three species in that in a flood plain meadow it would found to be mono-carpic with a life-strategy similar to *Draba incana*. Although mature individuals had a much shorter life (2 years), they produced large numbers of seed in their second year. Conversely, the same species growing in a sub-alpine meadow was found to have a much longer life-span and to be poly-carpic, producing relatively small numbers of seed over several years; that is, under these more extreme conditions the behaviour of the population was very similar to *Polygala amarella*.

It is clear from this study that within perennial species growing in grassland communities, at least in Upper Teesdale, a wide variety of life strategies exist. It appears that each strategy is able to maintain the size of each population despite the fact that the plants suffer the ravages of sheep, which for Gentiana verna, and to a lesser extent Carex ericetorum, prevents reproduction by means of seed production. In addition to this, the species have been able to survive for a very long time and in various and varying climatic conditions.

Table a

	Viola rupestris	Viola riviniana	Viola rupestris x riviniana	Gentiana verna	Polygala amarella	Draba incana	Carex ericetorum	Linum catharticum
(a) No. plants in original population recorded Aut. 1968	93	168	None	260	214	204	60	-
(b) No. plants present Aut. 1972 (Quadrats record Aut. 1968)	120	282	None	310	225	301	56	-
(c) Annual mortality (excluding first year seedlings)	14	13	12	30	31	38	26	100
(d) Annual recruitment - vegetative shoots	16	16	18	37	None	None	36	None
(e) Annual recruitment - seedlings	13	8	None	None	54	157	None	-

	Viola rupestris	Viola riviniana	Viola rupestris x riviniana	Gentiana verna	Polygala amarella	Draba incana	Carex ericetorum	Linum catharticum
(f) Annual mortality - seedlings	35	20	None	None	29	63	None	76
(g) Annual seed production	73	56	None	1,183*	377	2,541	26	2,556
(h) Half-life	9	12	14	4	4	3	4	-
(i) % Flowering plants	18	11	11	7	29	13	8	100
(j) Mean flowers/flowering plant	1.10 (0.21)**	1.16 (0.33)**	0.35 (0.27)**	1	-	-	-	-
(k) Mean fruits/flowering plant	0.50 (0.08)**	0.46 (0.02)**	None	1	7.65	10.32	3.33	3.4
(l) Mean seeds/capsule	8.32	9.1	None	169*	1.7	18.94	1	7.5

All figures in rows c-f are expressed as a rate per 100 plants in the population

* These values are based on capsules collected from inside an exclosure

**( )Value for the production of open flowers and fruits from open flowers

CHAPTER ELEVEN

CONCLUSION

The survival of the 'Teesdale rarities' has been discussed on a number of occasions, including Godwin (1956), Pigott (1956), Bellamy et al. (1969), Bradshaw (1970), Jeffrey (1971) and Johnson (1971). Several different environmental factors, including climate, the nutrient status of the soil and the unique bedrock, have been considered to be important to the survival of the 'rarities', both through the forest maximum and up to the present day (see also Chapter two). It is now generally accepted that many of the rarities are relicts from the late-glacial flora. This has been confirmed by Turner et al. (1973) who found evidence of the presence of some of the species through the forest maximum.

The most important feature allowing survival through the forest maximum seems to be the fact that at no time was the canopy completely closed. Throughout this period, herb pollen ratios were much higher than in the lowlands and Turner et al. interpret this as meaning that: 'the woods were considerably more open than those of the lowlands, open enough to allow a varied herbaceous flora to flourish and contribute approximately a third of the total pollen. Although habitats for the rare species may have been more restricted than during the late-glacial, development of woodland on the Fell could at the most only have decreased the areas available for them, certainly not destroyed them altogether.'

The data presented here clearly illustrate the variety of life-strategies, exhibited by the species studied. The fact that *Draba incana*, under present environmental conditions, requires open habitats for the successful establishment of seedlings, suggests that these open or eroding habitats must have been present throughout the post-glacial. Similarly, *Viola rupestris*, which appears to be near the limits of its tolerance in a closed grass sward, almost certainly required eroding or open conditions for its survival.

The other 'rarities' included in this study, *Polygala amarella*, *Gentiana verna* and *Carex ericetorum* are all able, in the short term at least, to survive in a closed sward. However, for the long term survival of *Gentiana verna*, open areas may have been required so that seedlings could become established.

Turner et al. (1973), in discussing the survival of *Gentiana verna*, suggests that during the forest maximum it was likely to have been found growing along the streams where, locally, there was freedom from shade. The fairly widespread occurrence of *Gentiana verna* today in Upper Teesdale, Elkington (1972), is probably related to its ability to produce large numbers of seeds and to reproduce vegetatively. The former of these methods of reproduction would allow the species to colonise suitable new habitats as the forest was cleared, the latter allowing its survival in these areas even when environmental factors, such as grazing, prevented the production of seed.

Carex ericetorum, on the other hand, is a species which is found in the Pine forests of European Russia together with *Galium boreale* and *Antennaria dioica*, two other 'rarities' also occurring in Teesdale, Keller (1927). Watt (1971b), considers Carex ericetorum to be one indicator of former pine forest and in Teesdale it appears that it is '. . . restricted to the sugar limestone, the very areas where pine grew best during much of the post-glacial', Turner et al. (1973).

Polygala amarella is able to survive by the production of seed and seedling establishment in the closed grazed sward. It is likely that this species survived the period of the forest maximum under openings in the canopy. Certainly, Pigott (1956), observed that, 'Polygala amarella and Gentiana verna have both been noted in fruit under small openings in the canopy of Picea abies forest in the Alps'.

For both Carex ericetorum and Polygala amarella, the production of small numbers of large seed probably provides an initial energy source, which enables seedlings to become established under shade. This cautious policy of seed production together with, in Carex ericetorum vegetative reproduction, is important to the survival of these species under present day conditions. For Polygala amarella, in particular, the large seed, by reducing the risk of mortality in the early stages of seedling establishment, aided survival in the closed, grazed sugar limestone turf.

The fact that many of the rare plants growing in the grazed turf today lie close to springs and flushed areas may not be accidental. In an open forest it is likely that browsing animals would visit the springs for water and may have grazed the open areas nearby, helping to maintain the open conditions. As already indicated for Gentiana verna, clearance of the forest probably allowed the populations, surviving in the openings in the canopy, to expand.

However, the relatively low reproductive potential of some species, as revealed in their reliance on a cautious policy of investment, (both for vegetative reproduction and/or the production of seeds, Viola rupestris, Carex ericetorum, Polygala amarella and Viola rupestris x riviniana) may be responsible for the very limited distribution of these species in the sugar limestone grasslands in Upper Teesdale. For Viola rupestris and Draba incana, the presence of suitable habitats for colonisation is also important.

Grazing animals, by helping to reduce the competitive ability of some of the more vigorous species, are probably important to the maintenance of the more sensitive rare plant populations. However, at the present time, the level of grazing is such that in the long term it could be detrimental to the populations. The production of seeds and, therefore, the replenishment by means of seedling establishment, is not only curtailed in Gentiana verna and Carex ericetorum, but also in Primula farinosa and Tofieldia pusilla, where few inflorescences survive the ravages of sheep.

This has implications for the long term survival of the species by preventing the exchange of genetic information, which might allow adaptation to changing environmental conditions. Perhaps also of importance, is the reduction of the reproductive ability of the species, which could prevent the expansion of the population into new, suitable habitats. As we have seen, particularly for Gentiana verna, the production of seed provides a very large potential source of new recruits.

Over the period of this study none of the species which were recorded showed a decline in numbers. Therefore, there would appear to be no requirement of specific management aimed at conserving any of these species. However, the time-scale is short when compared with the time taken for complete replacement of the population. Even for Gentiana verna, which is among the shortest lived perennial herbs studied, this may take six or more years. For Viola rupestris, this period is even longer and it may be many years before there is any noticeable decline in numbers.

An appreciation of the different life-strategies of individual plant species will aid the planning of management, aimed specifically at their conservation. For example, it will be possible to decide whether material can be collected for research, and if so, what the implications might be for the survival of the population. Also, it should help in deciding, if a species appears to be disappearing, how best to reverse the decline. This might be achieved by direct interference in the plant's life-cycle, either by-passing stages known to have a high risk of mortality attached to them, or providing conditions where successful establishment of new recruits is more likely.

In a habitat like the sugar limestone grasslands of Upper Teesdale, where there are a large number of rare plant species, management, aimed at providing conditions suitable for successful replenishment of all the populations, is required. In this context it is convenient to use the classification adopted by Watt (1971b). He grouped the rare species growing in the Breckland into three categories, depending on their social status:

Group 1. Species which persist in the mature phase. All maintain themselves vegetatively.

Group 2. Species which survive the establishment/building phase but succumb to competition with grasses.

Group 3. Small plants, often annuals or biennials, which require bare patches of ground or short, open turf.

Of the species studied *Gentiana verna*, *Carex ericetorum*, *Viola riviniana* and *Viola rupestris x riviniana* are all in Group 1. *Viola rupestris* might also be included in Group 1, but in view of its apparent sensitivity to competition, even in the closely grazed turf on Widdybank Fell, should perhaps properly come into Group 2. *Polygala amarella* must also be added to Group 1 as it is able to survive in the closed grazed sward, but in this case reproduction is by seed production.

Draba incana and *Linum catharticum* clearly belong to Group 3.

Watt considered that Group 1 required no specific management policy, and so long as the grazing does not become so intense as to cause a reduction in the size of the populations, this would appear to be true as long as the existing level of grazing is not altered.

Groups 2 and 3 require the creation of open habitats and need to be able to produce seed. Watt suggests that grazing might be allowed only after seed-set. However, it is clear from this study that species requiring open conditions are well adapted and able to produce sufficient seed to survive, (*Draba incana* and *Viola rupestris*) and that all that is required are the open conditions. The friable nature of the subsurface weathered rock, and mole activity, appear to fulfil this requirement.

Many of the 'Teesdale rarities' have survived in Teesdale for a very long time. They are able to maintain their populations today under the present management regime, and as long as conditions do not change they should continue to survive. It is hoped that the present study, by giving some insight into the population behaviour of some of the plant species growing in Teesdale, will help future management decisions to take into account the requirements of the individual species.

REFERENCES

ANDREWARTHA, H. G. (1961). Introduction to the study of animal populations. Methuen.

ANDREWARTHA, H. G. and BIRCH, L. C. (1954). The distribution and abundance of animals. University of Chicago Press, Chicago.

ANTONOVICS, J. (1972). Population dynamics of the grass *Anthoxanthum odoratum* on a zinc mine. J. Ecol. 60, 351-365.

BACKHOUSE, J. and BACKHOUSE, J. Jun. (1843). An account of a visit to Teesdale in the Summer of 1843. Phytologist 1, 892-895.

BACKHOUSE, J. Jun. (1844). Notes of a Botanical ramble in Yorkshire, in the Summer of 1844. Phytologist 1, 1,065-1,069.

BAKER, J. G. and TATE, G. R. (1868). A new flora of Northumberland and Durham. Natural History Transactions of Northumberland and Durham, II, 1-316.

BAYFIELD, N. G. (1971). Some effects of walking and skiing on vegetation at Cairngorm. Symp. Br. Ecol. Soc. No. 11, 469-485.

BEATTIE, A. J. (1969). Studies in the pollen ecology of *Viola*. I, Pollen-content of stigmatic cavities. Watsonia 7, 142-156.

BELLAMY, D. J., BRIDGEWATER, P., MARSHALL, C. and TICKLE, W. M. (1969). Status of the Teesdale Rarities. Nature 222, 238-243.

BLAKE, A. K. (1935). Viability and germination of seeds and early life history of prairie plants. Ecol. Monog. 5, 405-460.

BLISS, L. C. (1962b). Adaptations of Arctic and Alpine plants to environmental conditions. Arctic 15, 117-144.

BRADSHAW, M. E. (1970). The Teesdale flora: in Dewdney, J. (ed.) Durham County and City with Teeside, British Association, Durham, 141-152.

CLAPHAM, A. R., TUTIN, T. G. and WARBURG, E. F. (1962). Flora of the British Isles 2nd Edition. Cambridge U.P.

DARWIN, C. R. (1859). The origin of species. 6th Edition 1872 as reprinted in 1878.

DEEVEY, E. S. (1947). Life tables for natural populations of animals. Q. Rev. Biol. 22, 283-314.

ELKINGTON, T. T. (1962). Experimental taxonomy of some members of the Teesdale Flora. Durham University Ph.D. Thesis.

ELKINGTON, T. T. (1963). Biological Flora of the British Isles: Gentiana verna L. J. Ecol. 51, 755-767.

ELKINGTON, T. T. (1972). Variation in Gentiana verna L. New Phytol. 71, 1,203-1,211.

FEARN, G. M. (1971). Biosystematic studies of selected species in the Teesdale Flora. Ph.D. Thesis, University of Sheffield.

FLORA EUROPAEA (1964). Ed. TUTIN, T. G., HEYWOOD, V. H., BURGES, N. A., VALENTINE, D. H., WALTERS, S. M., and WEBB, D. A. Cambridge U.P.

GADGIL, M. and BOSSERT, W. H. (1970). Life historical consequences of natural selection. Am. Nat. 104, 1-24.

GODWIN, H. (1956). The History of the British Flora: a factual basis for phytogeography. Cambridge.

HARBERD, D. J. (1961). Observations on the population structure and longevity of Festuca rubra. New Phyt. 60, 184-206.

HARBERD, D. J. (1962). Some observations on natural clones in Festuca ovina. New Phyt. 61, 85-100.

HARBERD, D. J. (1963). Observations on natural clones of Trifolium repens. New Phyt. 62, 198-204.

HARPER, J. L. (1964). The individual in the population. J. Ecol. 52. (Suppl.) 149-158.

HARPER, J. L. (1967). A Darwinian approach to plant ecology. J. Ecol. 55, 247-270.

HARPER, J. L. (1971). Grazing, fertilizers and pesticides in the management of grassland. Symp. Br. Ecol. Soc. No. 11, 15-31.

HARPER, J. L. and McNAUGHTON, I. H. (1962). The comparative biology of closely related species living in the same area. VII Interference between individuals in pure and mixed populations of Papaver species. New Phytol. 61, 175-188.

HARPER, J. L. and SAGAR, G. R. (1953). Some aspects of the ecology of buttercups in permanent grassland. Proc. 1st Br. Weed Control Conf. 256-264.

HARPER, J. L. and WHITE, J. (1970). The dynamics of plant populations. Proc. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeck, 1970) 41-63.

HARPER, J. L. and WHITE, J. (1974). The demography of plants. A. Rev. Ecol. Syst. 5, 419-463.

HARVEY, M. J. (1962). The cytotaxonomy of some rostrate violets. University of Durham Ph.D. Thesis.

JEFFREY, D. W. (1971). The experimental alteration of a Kobresia-rich sward in Upper Teesdale. Symp. Br. Ecol. Soc. No. 11, 79-89.

JOHNSON, G. A. L., ROBINSON, D. and HORNUNG, M. (1971). Unique bedrock and soils associated with the Teesdale Flora. Nature 232, 453-456.

JONES, A. V. (1973). A phytosociological study of Widdybank Fell in Upper Teesdale. Ph.D. Thesis, University of Durham.

KAY, S., and HARPER, J. L. (1974). The regulation of plant and tiller density in a grass sward. J. Ecol. 62, 97-105.

KELLER, B. A. (1927). Distribution of vegetation on the plains of Duropean Russia. J. Ecol. 15, 189-233.

KNUTH, P. E. O. W. (1906-09). Handbook of flower pollination. Based upon Hermann Müller's work the fertilization of flowers by insects. Translated by J. R. A. Davis. Oxford.

LANGER, R. H. M. (1956). Growth and nutrition of Timothy (Phleum pratense) I. The life-history of individual tillers. Ann. Appl. Biol. 44, 166-187.

LANGER, R. H. M., RYLE, S. M. and JEWISS, O. R. (1964). The changing plant and tiller population of timothy and meadow fescue swards. I. Plant survival and the pattern of tillering. J. app. Ecol. 1, 197-208.

MANLEY, G. (1936). The climate of the Northern Pennines: the coldest part of England. Qu. J. Roy. Met. Soc. 62, 103-115.

NEWMAN, E. I. (1963). Factors controlling the germination date of winter annuals. J. Ecol. 51, 625-638.

PIGOTT, C. D. (1956). The vegetation of Upper Teesdale in the North Pennines. J. Ecol. 44, 545-586.

PIGOTT, C. D., and WALTERS, S. M. (1954). Discontinuous distribution of species of open habitats. J. Ecol. 42, 95-116.

PUTWAIN, P. D. (1970). The population dynamics of Rumex acetosa and Rumex acetosella. Proc. 10th Br. Weed Control Conf. 1, 12-19.

PUTWAIN, P. D. and HARPER, J. L. (1970). Studies in the dynamics of plant populations. III The influence of associated species on populations of Rumex acetosa and Rumex acetosella in grassland. J. Ecol. 58, 251-264.

RABOTNOV, T. A. (1960). Some problems in increasing the proportion of leguminous species in permanent meadows. Proc. 8th Int. Grassld. Congr. 260-264.

RIDLEY, H. N. (1930). The dispersal of plants throughout the world. . . . Ashford.

SAGAR, G. R. (1959). The biology of some sympatric species of grassland. D.Phil., University of Oxford.

SAGAR, G. R. (1970). Factors controlling the size of plant populations. Proc. 10th Br. Weed Control Conf. Vol. 3, 965-979.

SAGAR, G. R. and HARPER, J. L. (1961). Controlled interference with natural populations of Plantago lanceolata, Plantago major and Plantago media. Weed Res. 1, 163-176.

SALISBURY, E. J. (1942). The reproductive capacity of plants. Bell, London.

SARUKHAN, J. (1971). Studies on plant demography. Ph.D. Thesis, Bangor.

SARUKHAN, J. (1974). Studies on plant demography: Ranunculus repens, Ranunculus bulbosus and Ranunculus acris. I. Reproductive strategy and seed population dynamics. J. Ecol. 62, 151-177.

SARUKHAN, J. and HARPER, J. L. (1973). Studies on plant demography: Ranunculus repens, Ranunculus bulbosus and Ranunculus acris. I. Population flux and survivorship. J. Ecol. 61, 675-716.

SELMAN, M. (1970). The population dynamics of Avena fatua (wild oats) in continuous spring barley: desirable frequency of spraying with Tri-allate. Proc. 10th Br. Weed Control Conf. 3, 1,176-1,188.

SHIMWELL, D. W. (1969). The status of the Class Elyno Sesterietea. Br.-Bl. 1948 in the British Isles. Mitt. Flor. Soziol. Arbeitsgem. NF.14, 309-321.

STREETER, D. T. (1971). The effects of public pressure on the vegetation of chalk downland at Box Hill, Surrey. Symp. Br. Ecol. Soc. No. 11, 459-468.

TAMM, C. O. (1948). Observations on reproduction and survival of some perennial herbs. Botaniska Notiser 3, 305-321.

TAMM, C. O. (1956a). Composition of vegetation in grazed and mown sections of a former hay meadow. Oikos 7:I, 144-157.

TAMM, C. O. (1956b). Further observations on the survival and flowering of some perennial herbs. Oikos 7:II, 273-292.

TAMM, C. O. (1972a). Survival and flowering of some perennial herbs. II, The behaviour of some orchids on permanent plots. Oikos 23, 23-28.

TAMM, C. O. (1972b). Survival and flowering of some perennial herbs. III, The behaviour of *Primula veris* on permanent plots. Oikos 23, 159-166.

TURNER, J. (1970). Vegetational History: in Dewdney, J. (ed.) Durham County and City with Teesside, British Association, Durham, 123-133.

TURNER, J., HEWETSON, V. P., HIBBERT, F.A., LOWRY, K. H. and CHAMBERS, C. (1973). The history of the vegetation and flora of Widdybank Fell and the Cow Green reservoir basin, Upper Teesdale. Phil. Trans. Royal Soc. Lon. 265, 327-408.

VALENTINE, D. H. (1949). Vegetative and cytological variation in *Viola riviniana* Rehb., in Wilmott, A. J. (Ed.) British Flowering Plants and Modern Systematic Methods: B.S.B.I. Conference Report 1. 48.

VALENTINE, D. H. (1965). Ed. Natural History of Upper Teesdale, Northumberland and Durham Naturalists' Trust, Newcastle upon Tyne.

VALENTINE, D. H. and HARVEY, M. J. (1961). *Viola rupestris* Schmidt in Britain. Proc. B.S.B.I. 4(2), 129-135.

VALENTINE, D. H. and HARVEY, M. J. (1963). Variation in *Viola rupestris* Schmidt. Veriff. Geobot. Inst. Rübel, Zurich, 36, 157-163.

WATT, A. S. (1960). Population changes in acidiphilous grass-heath in Breckland, 1936-57. J. Ecol. 48, 605-629.

WATT, A. S. (1971a). Factors controlling the floristic composition of some plant communities in Breckland. Symp. Br. Ecol. Soc. No. 11, 137-152.

WATT, A. S. (1971b). Management programme for the Breckland rarities. J. App. Ecol. 8, 593-609.

WELLS, T. C. L. (1967). Changes in a population of *Spiranthes spiralis* (h.). Chevall at Knocking Hoe National Nature Reserve, Bedfordshire, 1962-1965. J. Ecol. 55, 83-99.

WELLS, T. C. E. (1971). A comparison of the effects of sheep grazing and mechanical cutting on the structure and botanical composition of chalk grassland. Symp. Br. Ecol. Soc. No. 11, 497-515.

WILLIAMS, O. B. (1970). Population dynamics of two perennial grasses in Australian semi-arid grassland. J. Ecol. 58, 869-875.