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"Further studies in the population dynamics of some Teesdale plants"

Being a Thesis submitted for the degree
of Doctor of Philosophy of the University
of Durham by

Robert Berkeley Gibbons

September, 1978.

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ABSTRACT

The population dynamics, life-histories, and reproductive strategies of a number of rare plants in the Upper Teesdale National Nature Reserve have been studied in detail over a three year period. Results from a seven year period have been analysed, and information presented on the changes in numbers, mortality rates, recruitment rates, and reproductive behaviour of *Viola rupestris*, *Polygala amarella*, *Gentiana verna* and *Viola rupestris x riviniana* with particular reference to different site conditions. The mortality patterns of even-aged cohorts of plants have been followed, and mathematical models fitted to their rates of decline.

The relative contributions of sexual and vegetative reproduction to the population numbers have been analysed, and the different reproductive strategies related to different environmental conditions. Life-cycles have been constructed for some species, and those points of the life-cycle where the greatest losses of plants occur have been revealed.

The study has also sought to analyse any effects on the rare plant populations caused by the presence of the recently-constructed Cow Green reservoir, and future management of these rare plants is considered in the light of the information collected.

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Finally, I am greatly indebted to Mrs. Beryl Crowther for typing this thesis, to my wife, Liz, for her considerable forbearance and encouragement during its production, and to parents and parents-in-law for constant support.

This study has relied considerably on the work of others. The author's recording sites and methods followed directly those used by Dr. J.P. Doody*, which were originally established by Miss M.E. Watson. Wherever appropriate, to gain the maximum advantage of a longer period of study, the results of these previous studies have been used in analysis. Normally raw data have been taken and analysed together with the author's own results; wherever figures have been used direct from Dr. Doody's thesis, they have been quoted as such. I am very grateful to Dr. Doody for permission to use his data in this way.

My own recording covered the period Autumn 1972 to Autumn 1975 only.

I am also grateful to Mr. P. Marren, who succeeded me as Research Assistant on the same study, for permission to use charts on to which he had abstracted my field data for <u>Polygala amarella</u> for 1975, and for allowing me to check the correctness of my 1975 records against his 1976 records, to observe whether any plants not seen in the late autumn of 1975 had been refound in spring 1976.

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* Doody, J.P. (1975). Studies in the population dynamics of some Teesdale plants, Ph.D. Thesis. University of Durham.

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Chapter One

Plant population dynamics

Surprisingly few long and detailed studies of the dynamics of natural plant populations have been published. Plant populations may often be considerably easier to study than animal populations, since most higher plants remain where they are and can be easily isolated and counted, yet much of our knowledge of the processes of population dynamics comes from studies of animals, including large mammals (e.g. Murie, 1944; Green and Evans 1940, Edmonson 1945). Whilst part of the reason for this neglect lies in the problems of the extreme plasticity of plants, and frequent difficulty in defining and distinguishing effective reproductive units (Harper, 1967), clearly this is not the whole answer. Many plant species lend themselves readily to population analysis because of their clearly-separated, similarly-sized individuals, and the few studies that have been made have shown that the difficulties are often readily overcome or avoided in practice, and the results very worthwhile (e.g. Tamm, 1948, 1956, 1972 and 1972a; Rabotnov, 1960; Sarukhan and Harper, 1973). Much of the early lack of research probably stems from a failure to appreciate the dynamic characteristics of superficially-stable vegetation, and the potential for elucidating information on component species by specific studies.

Over the last 20 years or so, interest in the population dynamics of plants has increased considerably, though the great majority of studies have been of a short-term nature, lasting for one to three years. The questions that such studies seek to answer include:-

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1. How does the total number of individuals in a population change over a given time?
2. What is the mechanism of this change in terms of recruitment and mortality?
3. What is the age-structure of the population?
4. What is the life-expectancy (or other measure of length of life) of individuals in the population?
5. How are losses and gains of new plants or potential plants related to the life-cycle of the plant?
6. What is the relationship between age and reproductive ability of the plants, and what is the reproductive strategy of the species?

For more complete studies, additional information needs to be sought on the detailed biology and life-cycle of the subjects, and on the relationship between the population and the environment. It may also be possible to predict future trends in population numbers, and to understand past histories.

There are, essentially, two main ways in which adequate information on the population biology of plants may be collected. The quickest way may be to sample a population at a single point in time, and to use the resulting information on the age-structure of the sample to predict other population parameters. This method has often been used for animal populations (e.g. Murie, 1944; Caughley, 1965 and 1966) and for woody plant species. Blackburn and Tueller (1970) observed the age structure of populations of Pinyon Pines (Pinus monophylla) and Junipers (Juniperus osteosperma) under different conditions using direct methods of measurement, dividing the age structure of the populations into 6 "maturity classes" and relating this to colonisation processes. In another example, (Henry and Swan, 1974) the history of a virgin forest was carefully reconstructed for a period of more than 300 years by using age-structure data in combination with other observable features of the forest.

Such studies are, predictably, very rare on herbaceous plants because of the difficulties of ageing material. In one classic early study, Linkola (1935) estimated the age distribution of a number of different herbs in a Finnish meadow using morphological characteristics as an indication of the age of individuals. It is possible to use the information from such a study to predict the mortality pattern of the species by equating the observed age distribution with a survivorship curve (e.g. Caughley, 1966; Harper 1977) and thence gaining a measure of the rate of turnover of the population. However, such a calculation involves the direct assumption that recruitment to the population has remained more or less constant over the time period involved in the production of that particular population. Although such an assumption may be correct, it is frequently not, and - as will be shown in later Chapters - recruitment can vary considerably even in populations of plants which are known to be long-established. The dangers are elegantly illustrated by Harper (1977) who uses the same set of theoretical values for an age-structure of a population to show that the population could either be considered as a stable one with regular annual recruitment and age-independent mortality, or as one with an exponentially increasing rate of recruitment and no mortality, or as something in between the two extremes. Without supporting data, therefore, such studies are unlikely to be very revealing with regard to the dynamics of the population.

The second major way in which information about the dynamics of a population may be gathered involves the more tedious and lengthy method of following the fates of all individual plants of particular species in a sample population, as has been done in the present study. On its own, this procedure yields information on changes in population numbers, rates of recruitment and mortality, life expectancy of individuals and rate of turnover of populations, as well as much valuable information on the life-strategy of the species. If additional information is gathered on the rate of production of seeds, or other propagules, and the fate of these propagules can be followed, then a reasonably clear picture of the life-cycle and population dynamics of a particular species in a particular habitat may be built up.

The pioneer studies in this field, and the longest studies of population dynamics of herbaceous perennials published, were carried out by Tamm (1948, 1956, 1972, 1972a). In 1942, he began observations on small fixed quadrats in meadows and woodland in which a number of species were studied in detail. His most recent papers (Tamm 1972, 1972a) include data up to 1971. In each case, the initial populations were composed of individuals of unknown age. The position of all plants of those species under study were carefully marked and their fates followed over succeeding years. New additions were recorded, and their fates as individuals of known age followed by subsequent annual recordings. In 1956, he presented the results of 13-14 years of study on _Anemone hepatica_, _Sanicula europaea_, _Filipendula vulgaris_, _Centaurea jacea_, and a mixed meadow plot. Several points of particular interest emerged: Anemone hepatica, Sanicula europaea, and Filipendula vulgaris all more or less maintained their population numbers, but the study revealed that there was quite a rapid turnover of plants within the populations, and that both seedlings and vegetative additions were being recruited and were dying. In contrast, Centaurea jacea was shown to be a declining population, with the process of decline clearly shown; mortality remained constant but no new plants appeared. In all cases, the considerable longevity of individuals is a surprising feature. Harper (1967) re-presented some of Tamm's data in the form of depletion curves for the original mixed-age population. By analogy with radioactive decay rates, he was then able to calculate 'half-lives' for each species population, based on the fact that mortality was age-independent, and therefore the depletion curves were linear. When appropriately used, these figures provide valuable insight into the turnover rates of populations and act as useful bases for comparisons between species. Using Tamm's data, Harper showed that the initial population of Sanicula europaea had a half-life of over 50 years, Filipendula vulgaris had a half-life of 18.4 years, and the declining Centaurea jacea had a half-life of c.1.9 years. Additionally, Tamm showed that the percentage of plants flowering varied considerably from year to year, that many plants flowered repeatedly in successive years, and that the pattern of recruitment of seedlings into the population was by no means regular.

In 1972, further results of Tamm's studies on his original, and other, quadrats were published (Tamm 1972, 1972a). In some instances, these provide records of populations stretching over nearly 30 years, and therefore provide unrivalled information both on the behaviour of members of the population, and the behaviour of the whole population, particularly in relation to changing environmental conditions. It is of particular interest to see that 18 individuals of Dactylorchis sambucina were still surviving in 1971 out of the original 1942 population of 52, and that some of these are still flowering, despite a general reduction in flowering percentage of individuals in the plot; and 15 individuals of Listera ovata out of a 1944 population of 22 were surviving, with a very high percentage still flowering. It is likely, therefore, that individuals of these 2 species of orchid may attain ages of well over 30 years, and, under reasonably favourable conditions, produce flowers regularly. It is interesting that in this study, and Tamm's study on Primula veris (1972a) there are the effects of significant local and general environmental changes (with the possible exception of P. veris site III) superimposed on the inherent mortality and recruitment patterns of the species which have affected the observed dynamic patterns. Because species in more stable situations frequently show such strikingly stable rates of mortality (e.g. Tamm 1956; Sagar 1959; Sarukhan and Harper 1973), not only independent of the age of the plant but also of the different annual weather conditions, it seems that the survival of established individuals is much more affected by particular local conditions such as grazing, mowing, drainage, shading, etc., than by the weather in different years, expect perhaps where extreme weather is encountered.

Whilst Tamm's studies provided considerable information on the aspects described above, there were less data on the detailed processes of seed production and establishment, clonal growth, and seasonal changes in mortality and recruitment rates.

Records were only taken once per year, so that some of the shorter-lived phenomena were inevitably missed. In a shorter, but more detailed study, Sagar (1959, from Harper 1967; Sagar and Harper, 1960; Sagar 1970) observed populations of Plantago spp. in heavily-grazed grassland over a 2 year period. From frequent observations of newly-recruited seedlings of P. lanceolata, he was able to show that 2/3rds of the seedlings recruited during the 2-year period died before they were 12 months old, in contrast to the calculated half-life of the original mature plants of c. 3.2 years. Detailed studies of the early mortality of seedlings are rare, and studies that attempt to show pre-emergence losses are even rarer. "Germination" is generally recorded as having occurred when cotyledons are visible above ground, but as Harper (1977) points out, in reality this excludes information on mortality of seeds that germinate, but do not emerge. Other losses are sustained at the pre-germination stage by predation, damage, pathogen attack, loss of viability, etc. Studies that analyse the fate of seeds are also rare, and the difficulties are obvious, although many records emphasise the extremely low percentage of seeds that survive to produce new adults (e.g. Darwin, 1962; Salisbury 1942, Sagar 1970). Donald (1959) followed the fate of naturally sown seeds of Trifolium subterraneum and found that 92.1% of seedlings appeared in the first year after sowing, 6.3% in the second year, and 1.0, 0.52 and 0.07% in the third, fourth and fifth years respectively. Presumably, therefore, if this was a normal year, then the seedlings appearing in any one year are from seeds produced over several years. Naylor (1972) used an elegant "mark and recapture" technique on populations of Blackgrass (Alopecurus myosuroides). He added fluorescent paint-marked seeds to plots to the level of 10% of the estimated natural seed rain over 3 periods, and was able to observe the percentage of germinating seeds resulting from the marked seeds. He calculated that approximately 2/3rds (62-71%) of the seedlings emerging were from seeds less than one year old, and that seeds sown at different times did not make significantly different contributions to the following year's population. However, it is more or less certain that other species in other habitats will have quite different patterns of mortality and germination time in seeds, and few generalisations relevant here can be made from these isolated studies.

Once a seedling has emerged, it may be recorded by the normal methods. The detailed mortality patterns of these earliest stages of the growing plant have been recorded in most detail for annual plants where germination and seedling establishment play a relatively greater part in the life-cycles. Sharitz (1970) and Sharitz and McCormick (1973) present detailed figures for 2 winter annuals, Minuartia uniflora and Sedum smallii. In Minuartia uniflora, they show that, for every 1000 seeds, 210 remain available for germination and that 64 of these germinate (30%), and 11 (17%) become established. In Sedum smallii, 840 seeds remain available, 210 germinate (25%), and 33 become established (16%). The differences in seed survival are largely accounted for by differences in the methods of release of the seed, but in both plants a considerable loss rate is shown at, or soon after, seed germination. In a study of the winter annual Cerastium atrovirens on sand dunes, Mack (1976) in contrast found that there was minimal mortality amongst newly-germinated seedlings, perhaps because of the more stable, less harsh conditions of this study. The survivorship curve of a large cohort of seedlings (6504) was sharply negatively skewed, similar to that found by Beatley (1967) for various winter annuals in the Mojave desert.

In *Vulpia membranacea*, each plant was shown by Watkinson (1975) to produce only 1.7 mature seeds on average, of which 90% germinated, and 69% of the seedlings survived to flowering.

Clearly, the phase from seed production to seedling establishment is a very critical phase in the life-cycle of plants that reproduce by seed, and there are many different patterns shown in the survivorship of these stages. These differences frequently reflect the reproductive strategy of the plant; for example, a plant may produce many small seeds of which a minute percentage survive to each successive stage (e.g. orchids), or fewer larger seeds from which a higher proportion survive (e.g. *Vulpia membranacea*). Similarly, the environment of a particular species is likely to affect its pattern of seed and seedling mortality.

Although, in general, the greatest percentage losses of potential new plants occur in the seed and seedling stages, it is of particular interest to follow the fate of established seedlings on to reproductive maturity. In perennials, the situation may be quite complex in that, of those individuals that become apparently mature, many do not flower at first, some may flower and then die, and a surprising number persist for many years, eventually dying without flowering (see Chapters 4-7). At the same time, a series of generations are overlapping. As longer-term information on these aspects of the populations of plants is collected, it becomes possible to work out the overall flux and longevity of individuals and populations, and - in conjunction with information on fecundity - to gain a picture of the plant's reproductive strategy. Tamm's studies (Tamm 1948, 1956, 1972 and 1972a) provided the information that, whilst perennial herbs may be very long-lived, there is a surprising turnover continuing in the population. Additionally, he revealed the variable and irregular timing of flowering shown by individual plants. The number of times that a perennial, seed-producing plant flowers in its life is clearly of great importance for that plant's survival.

In most studies of perennial, polycarpic herbs, it has been shown that the rate of mortality of non-seedling plants is virtually independent of age (e.g. Tamm 1948, 1972, 1972a; Sarukhan and Harper, 1973; Antonovics, 1972; Foster 1964). In other words, once a plant has reached a certain state, usually attained during its first year of life, its likelihood of death seems to be determined by chance, and it is as likely to die at 2 years old as 10 years old. This observation, which sets plants aside from most animal populations, led Harper to present data on the survivorship of individuals as semi-logarithmic decay curves, likened to radioactive decay, (Harper, 1967). The particular exceptions to this study are a number of grass species, which it is of interest to consider here, although they are not directly relevant to this study. Williams (1970) followed the survivorship of cohorts of seedlings of Danthonia caespitosa and Chloris acicularis in different years. He found 1. that the survivorship curves rarely followed the Deevey (1947) Type II negative exponential curve, but were most commonly of the negatively-skewed Type III curve; and 2. that survivorship rates varied in different cohorts. This second feature is also shown by Anthoxanthum odoratum (Antonovics, 1972), and presumably somehow relates to the way a given climate acts on different-aged plants,

e.g. a dry summer period may increase mortality amongst 0-1 year olds, but not amongst 1-2 year olds to such an extent.
Canfield (1957) showed that several species of grass on rangeland in Arizona exhibited positively-skewed survivorship curves (Deevey Type I), with the lowest risk of death in middle age. These are the only published examples of such mortality patterns in perennial plants, although they are common in the animal world (including humans), and this mortality pattern may somehow relate to the increasingly dense tussock habit of the grasses.

The results of this study tend to fit the general pattern of age-independent mortality, with the possible exception of Viola rupestris (see sections 6.4 and 9), although it may not be applicable if seedlings under one year old are included. It is interesting that no apparent change in the rate of mortality as individuals approach or reach reproductive maturity is generally noted, although inspection of mixed-age population depletion curves only would obscure any such pattern.

Although the analogy of using exponential decay rate as a parameter of plant age cohorts should not be taken too far in view of the many and varied pressures that exist throughout a plant's life, it has proved to be of great value for comparing different species, or for comparing the same species in different conditions or areas, and it remains as one of the most interesting discoveries and tenets of plant population dynamics. It is of considerable interest that, in those few occasions where the mortality of one species has been studied at widely different localities, the half-lives have been of the same order. E.g. Ranunculus acris has been studied in river meadows in the U.S.S.R.

by Rabotnov (1958) with data recalculated by Sarukhan and Harper (1973), by Linkola (1935) in a Finnish meadow using age-structure data, and by Sarukhan and Harper (1973) in some detail in Welsh meadows. The calculated half-lives were 99 weeks for the Russian population, 65-100 weeks for the Finnish population (assuming more or less constant mortality, as discussed earlier), and 102 and 196 weeks for the Welsh populations. Thus, the differences are not large, despite the considerable climatic differences between the areas, and may indicate that climatic differences are not of great importance in determining the life span of plants - of certain species, at least - with the possible exception of plants growing at the edge of their range.

Within a given year, there may often be a definite seasonal effect observed on the mortality patterns. This has been reported, for instance, by Sagar (1959), re-presented by Sarukhan and Harper (1973) for populations of *Plantago lanceolata*, by Sarukhan and Harper (1973) for three species of *Ranunculus*, for *Anthoxanthum odoratum* by Antonovics (1972), for *Plantago rugelii* and *P. major* by Hawthorn and Cavers (1976) and for *Carex rostrata* by Bernard (1976) amongst others. In most cases, the highest mortalities were observed during the early summer months, except in the case of *Plantago major* in Canada, where mortality peaked in late summer (Hawthorn and Cavers, 1976). This seasonal mortality is ascribed to the additional demands made on the plant's resources, at the period of maximum growth, and competition with other plants, and may also depend on the demands made by preparing for reproduction, and by increased mortality following reproduction. All of these plants are relatively short-lived, and the seasonal variation may be less clear in longer-lived repeating flowerers.

The number of studies that have now been made on perennial herbs serve to illustrate the differences in life-cycles and strategies that exist between species, even between closely-related species and ones in very similar habitats. Gadgil and Bossert (1970) distinguish two very different strategies: the repeating producers, and the "big-bang" producers. Clearly, though, the differences may be considerably more subtle, and it is the study of environmental factors and how they operate at different stages of life-cycles that is one of the most fascinating features of plant population studies.

Sagar's studies on three *Plantago* species in permanent grassland under 3 management regimes (Sagar 1959) revealed how differences in management may affect the survival of different, though related, species, and how these changes in status may be brought about. He showed, for example, that *P. lanceolata* and *P. media* declined in an area grazed 3 out of 4 years, with hay cut in the fourth year, probably because of an inability to establish from seed, coupled with a short average life. *P. major* was common in an area that was cut with a scythe and periodically flooded, but it was eliminated from the grassland when cutting was stopped. A major flooding eliminated *P. lanceolata* from the area, and caused the subsequent establishment of large numbers of *P. major* seedlings. This type of study, outlined above, begins to give an insight into why plants grow where they do. In another study, Harper and Sagar (1953) were able to show that the 3 species of *Ranunculus*, *R. acris*, *R. bulbosus* and *R. repens* were distributed in a particular way, apparently depending on their ability to establish seed in certain conditions, and their clonal growth capacities. On old ridge and furrow grassland, they found that *R. repens* was confined to the damp bottom of the furrow, R. acris occupied an intermediate position, and R. bulbosus occupied the drier tops of the furrows. They showed that the seeds of each were best able to establish in the conditions in which the adults were growing.

The difficulties of seed establishment in closed grassland or other vegetation are well-known (e.g. Cavers and Harper, 1967; Miles, 1972; Summerfield, 1973; Grubb, 1977), and very relevant to the present study, where most of the sites are located in closed grassland, and many of the species are of limited distribution in Britain. The relationship between present day distribution and abundance of a species, and seedling establishment is a fascinating but vexed question. As Harper (1977) points out, by the time a plant is established, the peculiarities of the microsite around the developing seedling (and possibly the whole site) have long since altered. Studies of the present day requirements of a species, coupled with knowledge of its spatial distribution, and information on its life-cycle may be able to provide evidence of why the species is established, but historical factors must also be taken into account. Plants in general, and the plants in this particular study, produce far more viable seed than is necessary to maintain their populations, for which only one new plant per adult is required. The greater bulk of this seed probably ends up in areas apparently suitable for its germination and survival, yet only a very small proportion survive.

It is clear that changes in the environment may have considerable effects on the life-cycle, mortality, establishment and consequent distribution of species. Tamm (1972) attributed changes in the mortality rate of various orchids in meadowland to changing agricultural practices, whereas in an earlier study (Tamm, 1956) he found that a declining population of

Centaurea jacea maintained a constant mortality rate, but showed considerably reduced flowering, with no new plants being produced. Rabotnov (1960) showed that Trifolium repens may have a completely different life-cycle under different environmental conditions. In a comparison of populations of this species in both subalpine meadows and low-lying river meadows, he found that the plants in sub-alpine meadows were polycarpic, flowering either every year or every 2 or 3 years, that they did not flower until they were 5 to 10 years old, and that some individuals reached 20 years old. In the lower-lying meadows, in contrast, the plants usually flowered once and died, within 2 years from germination, and consequently there was a much greater population flux. Presumably, this relates to the slower growth of individuals in the higher meadows, with the long pre-reproductive phase and low fecundity compensated for by repeated-producing, although other factors are, no doubt, operating.

Pigott (1968, 1970) elegantly correlated the wider distribution of Cirsium acaulon with climatic factors. He showed that a certain level of summer warmth was necessary for the production of fertile seed, and that the effect of this was reinforced by combination with fungal attack in cooler areas. Thus at the edges of its range, Cirsium acaulon is able to produce fertile seed in sufficient numbers to establish new plants only in exceptional years. Although not specifically observed, it may be that longevity is increased under more difficult conditions, as in the case of Trifolium repens.

The present study has been largely concerned with rare species, and attention has been focussed on the way in which small or very small populations maintain their numbers, in one case in the only British locality (Viola rupestris x riviniana) and in another case at the edge of the species range in Britain (Polygala amarella). This particular aspect of population dynamics has received relatively scant attention, perhaps because rare species make difficult experimental subjects. Wells (1967) observed a population of Spiranthes spiralis over a period of three years. He recorded much of interest on the general population dynamics of the orchid, but was unable to account for the population's decline in flowering performance and the factors governing flowering, nor to predict the optimum management for that particular species. Dring and Frost (1971) and Watt (1971) have considered environmental factors in relation to the management of rare species, although their work included little on population dynamics. Bradshaw and Doody (in press) have reviewed the literature on population dynamics studies in relation to rare plants, and shown the importance of such studies in formulating management plans for conservation of rare species, with particular reference to Upper Teesdale.

The present study seeks to understand the dynamics of the plants in these populations of rare plants, to see how the populations are changing, to understand the weak points in their life-cycle, and to relate their performance to different environmental conditions.

Chapter Two

Upper Teesdale : The environment of the study

2.1. Introduction.

Upper Teesdale is well-known, in many scientific circles, as a unique area in Britain. Some of the reasons underlying its unusual character are considered here in relation to the work that has been carried out for this thesis, in an attempt to explain the exceptional richness of its scientific interest, and to indicate the length of time that some of the species studied may have lived in their present habitats.

Upper Teesdale lies at about latitude 54°40'N on the eastern slope of the Pennines, around the headwaters of the Tees which flows eastwards from there to the North Sea. All the Teesdale studies presented in this thesis were made on Widdybank and Cronkley Fells (523M and 547M respectively), some 15-20 Kms. from the source of the river. The extraordinary richness and variety of the flora has been known to botanists for a considerable period, although the detailed knowledge of species has been added to more or less continuously (e.g. Bradshaw and Jones, 1976), and new species are still being discovered, (e.g. Betula nana (Hutchinson, 1966) - although as Bradshaw (1970) points out, this is most probably a rediscovery of a very old record; Carex aquatilis, discovered in 1968 (Proctor, 1972) at a site where it was soon flooded by the rising reservoir, but rediscovered a few years later at a site lower down the river (Holmes, 1976); or Grimmia agassizii (Holmes 1976a), an extremely rare aquatic bryophyte in its only known English localities). John Ray first recorded Potentilla fruticosa from near High Force in 1718 (Ray, 1744), and during the nineteenth century Binks, Harriman, and later the Backhouses brought to light the extent and nature of the rich flora (Backhouse and Backhouse, 1843;

Backhouse, 1844). Baker and Tate (1868) listed over 30 rare plants in their Flora from an area of "something like 4 square miles" centred on Widdybank Fell, and later Pigott (1956) listed about 140 plants with some degree of rarity for the Upper Teesdale area, of which about half were higher plants. Many of the rarest plants are known only on the "sugar limestone" outcrops, whose interest was summarised by Ratcliffe (1977) thus: "The crumbling exposures of this rare type of rock, with their close-grazed and open grassy swards, and extensive systems of open calcareous flushes and mires, have an extraordinary number and abundance of rare or local montane plants."

2.2. The geological setting.

It seems reasonably certain that the underlying geology of Upper Teesdale is one of the major factors that has allowed the survival of so many rare plants there (e.g. Johnson et al, 1971), and therefore it is appropriate to consider this in reasonable detail as far as it relates to the areas of study.

At the end of the Carboniferous period, the quartz-dolerite Great Whin Sill was intruded as hot magma into the existing Carboniferous rocks, baking the sediments around it. More or less simultaneously, there began a period of hydrothermal mineralisation, which was to continue for some 100 m.y., and which resulted in the deposition of zinc, lead, fluorspar and barytes veins in the area. The Whin Sill came into contact with various Carboniferous limestones which were thus baked for some distance from the point of contact. Generally, the limestones were recrystallised to form marbles, as far as 25M from the point of contact, except for the darker pigmented limestones which did not recrystallise because of the higher proportions of carbonaceous matter supressing marmarization (Robinson, 1971).

The pure white Melmerby Scar limestone was recrystallised to saccharoidal marble, where it was within 25M of the Sill, and it is this rock that is frequently and aptly referred to as "Sugar limestone", and which only occurs in quantity on Cronkley and Widdybank Fells. The marble is composed of rounded, loosely-cemented grains of calcite varying from 0.5mm average size at the point of contact to 0.05mm at 18M above it.

Since the early Tertiary, there has been a long period of erosion, extending to the present day, which has removed overlying rocks and exposed the Sill and its associated marbles. About 1 million years ago, the Great Ice Age began, and thick ice sheets covered the region for an unknown period until about 10,000 years ago, when the climate warmed up and the ice finally retreated (Johnson, 1976). Some parts of Widdybank and Cronkley Fells are now overlain by drift of variable thickness, and many areas are covered by up to 12 feet of post-glacial peat (Johnson and Dunham, 1963). The marble is masked by the drift in some places, and by peat on the more impervious soils. Weathering of the marble has taken place below the surface, and the coarse-grained marble nearest to the Sill has broken up readily, although the rate of the whole process depends on the speed and extent of ground-water movement. "Sugar limestone" is thus chiefly a product of subsurface weathering of saccharoidal marble below a soil or peat mantle, exposed later by erosion of the surface layers. This resultant calcite sand is extremely easily eroded wherever the protective mantle is removed, and hence a cycle of subsurface weathering below thin soil, followed by erosion of the unstable calcite sand may have taken place in these outcrops during much of the post-glacial period, giving rise to a succession of open habitats. It is unlikely, though, that calcite sand deposits were present on these outcrops during the first stages of post-glacial plant colonisation, (Johnson et al 1971).

The soils that have developed over the limestones are influenced by the degree of contact with the limestone, and they vary from peat or peaty gleyed podsols, through brown earths and brown calcareous soils where the drift was thinner, to rendzinas over less than 30cms of drift. The whole geological setting and combination of soils is unique in Great Britain, and it is this inherent instability and rapid drainage of the calcite sand soils that has proved so important in the survival and continuing presence of many of the rare plants, (Johnson et al, 1971).

2.3. Climatic factors.

Upper Teesdale lies almost at the centre of the narrowest part of Britain, and its climate reflects this unusual position. Manley, (1936) provides records for the weather at Moor House (561M), 9 Kms west of Widdybank Fell, and points out that the records correspond well with figures for sea level in Southern Iceland (where a number of the Teesdale species occur). Doody (1975), in a comparison between Widdybank Fell (where there is now a Meteorological station) and Moor House, over the period 1968-1972 shows that Widdybank Fell was slightly warmer and drier than Moor House over that period. Pigott (1978) points out that the difference between the two stations is more or less as expected for their differences in altitude during the winter, but Widdybank is warmer than expected during the summer.

The general pattern is one of cold, rather snowy winters, very late springs, short cool summers, and cold autumns. The overall annual precipitation is usually 1500-1600mm (much lower than at comparable altitudes in the Lake District), with some of this falling as snow. Snow does not normally persist on the lower Fells beyond April, although night temperatures can be very low at this time. Manley's description of the weather on Dun Fell (848M) is very apt, although more severe than in our area: "We therefore form a conception of an excessively windy and pervasively wet autumn, a very variable and stormy winter with long periods of snow-cover, high humidity and extremely bitter wind, alternating with brief periods of rain and thaw. April has a mean temperature little above freezing point, and sunny days in May are offset by cold polar air, while the short and cloudy summer is not quite warm enough for the growth of trees" (Manley, 1945). The present tree line is estimated to be at about 600M, well above the level of the tops of Cronkley and Widdybank Fells (Pigott, 1978). Manley (1952) estimates the growing season at 450M in Teesdale to be from April 18th to October 23rd, while at 670M it extends from May 4th to October 16th. On Widdybank or Cronkley Fell it would therefore extend from about April 24th to October 20th, although some annual variation exists.

This general climate pattern is not unique in Britain, but is thought to have had a considerable effect on the survival of many of the rare plants in combination with other features of the area.

2.4 The history of the vegetation in Teesdale, and the survival of the rarities.

Forty years ago, it was generally considered that the Teesdale assemblage of plants had survived through the last ice-age on nunataks in the area (e.g. Wilmot, 1930; Blackburn, 1931). This has since been shown to be unlikely by the widespread demonstration that the late-glacial and immediately post-glacial vegetation of lowland England contained many plants now found in the Teesdale assemblage (e.g. Blackburn, 1952; Allison, Godwin, and Warren, 1952;

Godwin, 1975), and the realisation that the whole of the Teesdale area had been fully glaciated (Johnson and Dunham, 1963). Thus by far the most likely, and generally accepted, interpretation is that the present day flora of Upper Teesdale is, in most senses, a relict of the Late-Glacial flora (Godwin, 1956). It is of particular interest, therefore, to consider how the flora persisted to the present day.

It has been clearly demonstrated that trees grew in Upper Teesdale in the warmer post-glacial periods. Johnson and Dunham (1963) showed that birch, pine and hazel, in particular, grew at Moor House, and Turner et al. (1973) demonstrated the presence of a similar vegetation, with more pine, on Widdybank Fell. Between 6000 and 4000 B.C. the pine was gradually replaced by Oak and Alder as the dominant tree, and some forest cover persisted until the Iron Age, when increasing pressure from man, and changes in the climate, caused the disappearance of the remaining trees over an uncertain period, and grazing and other factors have effectively prevented regeneration of the trees ever since, although it is interesting that Squires (unpublished, quoted by Turner, 1970) showed that the vegetation on Cronkley Fell regenerated after an initial clearance, and was only cleared again after a considerable time during which woodland was again dominant.

Godwin (1949, 1956) and Pigott (1956) suggested, on theoretical grounds, that the rare plants had managed to survive because the tree cover had never become fully closed, and that some open habitats of varying size had always persisted. Confirmation of these theories came when the detailed studies of Squires, (1970; 1971) and Turner et al. (1973) showed that even during the Forest Maximum (6000-3000 B.C.), herbaceous pollen was at a considerably higher level than in lowland woodlands, and that out of the 16 rare plants from Pigott's (1956) list of rarities that had sufficiently diagnostic pollen, 11 had been shown to occur in Teesdale during the post-glacial period including the Forest Maximum. The absence of the other species does not, of course, mean that they did not occur. As Turner (1978) points out "when one considers the infinitesimal proportion of the total peat that has been examined, one realizes that the chances of finding the pollen of all the possible rare species were quite remote", and much must have depended on the abundance of the plant and its habitual method of pollination.

It is now possible, therefore, to build up a reasonable picture of the way in which some of the rarities survived from the end of the glacial period. As Johnson et al (1971) showed, the extreme erodibility and rapid drainage of the 'sugar limestone' soils has always provided open habitats which were not entirely suitable for tree growth. At the same time, various chemical factors in the soil were probably operating to reduce plant growth. Jeffrey (1971) has shown that the main factor reducing the growth of grasses in a kobresia-rich sward in Upper Teesdale appears to be lack of phosphate. Levels of phosphate were not found to be extremely low - comparable, for instance, to such soils as occur in dune slacks - but addition of phosphate promoted a considerable growth of grasses. Nitrogen alone had no such effect. Thus it seems likely that some other factor, or factors, are operating to affect the uptake of phosphate. He also showed that the levels of lead were very high in the soil, and he suggested that its presence might be affecting the phosphate uptake. In separate experiments, he showed that lead did have a considerable effect, but that Barytes did not. Other heavy metals may occur, particularly in localised patches, and they may have an effect on the relative competitive ability of different species. Further, Jeffrey and Pigott (1973) and Pigott (1978) showed that the thin soils lying directly over sugar limestone supported very little biomass even in the absence of grazing, and even where there was adequate soil water. Welch and Rawes (1969) pointed out the very high rate of drainage and frequency of drying-out in these soils, and, no doubt, this has always been a further factor in limiting tree growth and other vigorous plants.

It is clear that the present-day climate is likely to affect the composition of the vegetation. It may operate to reduce the growth of some of the more invasive species, but it may also operate to affect the life-cycles and establishment of such species. Bellamy et al.(1969) in a study of the productivity of some of the wetland Teesdale rarities in comparison with the productivity of various alpines and sub-arctic plants recorded by Bliss (1972), conclude that a productivity of 150 gms/M^2/annum is a critical figure in allowing the survival of rare plants, in conjunction with other factors. Because the climate was noticeably warmer during the Forest Maximum, it seems likely though that other factors, such as those described above, must have been responsible for maintaining the populations of the rare plants at that time. Bellamy et al. (1969) further suggest that "boundary instability" on a small or large scale may account for the survival of many of the rare grassland species. These are zones of vegetation instability, rather than continuous transition, and they showed that many rare species occurred in such zones, although at that time no complete picture of the vegetation of Widdybank Fell existed. Such boundary zones may consist of closed turf, but it is suggested that some environmental factor, - such as ground water - oscillates markedly in the zone. They suggest that the relatively large areas of single vegetation units containing rare species may be accounted for by the existence of large areas of boundary zones, possibly stabilised by man's influence.

It is probable that grazing has always been a factor promoting the survival of the rare plants in some areas. During the Forest Maximum, it is known that bison and other large herbivores, whose grazing and other life habits will have acted to keep areas free of trees and possibly promote the erosion of soils in small areas, were present. Since the forest clearance, grazing by wild and domesticated herbivores has prevented regeneration and maintained the closed turf. Turner et al. (1973) show that from about 1300-1100 b.c. at Weelhead, and 700-540 b.c. at Red Sike there has been grassland established over the better-drained limestone soils, and as both Turner (1978) and Roberts (1978) point out, there has been very little change, with the exception of those areas affected by mining, since then. So, grazed areas have probably always been present, and - for the last 2-3000 years - considerable areas of grassland have existed more or less constantly. Today, Widdybank Fell is grazed by a more or less constant flock of 400-450 sheep from March to November (Findlay, pers. comm.), by a small number of horses since 1973, and by an increasing number of rabbits. Cronkley Fell is heavily grazed by rabbits, and even in 1956, Pigott noted that the level of erosion seemed to be increasing. The effects of this grazing are manifold and difficult to quantify, although it seems likely that a marked reduction in overall grazing pressure on these Fells would lead to a reduction in the number and variety of rare species (Doody, 1975). In contrast some species may have disappeared as the grassland spread (Turner, 1978), and the present study indicates that some species would be more successful if given partial protection from grazing.

2.5 Summary.

It is probable that most of the species studied for this thesis, as members of the "Teesdale-assemblage" have survived since the immediate post-glacial period in or near their present habitat, for a variety of reasons, particularly associated with soil factors, grazing and climate. The grassland in which so many of the species occur, including those presented here, has probably been in existence for 2-3000 years in more or less its present form. The population dynamics of species growing in such a long-established habitat are of considerable interest.

Chapter Three

Methods

This study followed on from a study originated in 1968. The sites used for recording, and the methods of recording of basic data were identical. Sections 3.1 - 3.4 therefore follow Doody (1975) in their description of site selection, individual definition and data recording, other than where specific differences are noted. Sections 3.5 onwards are not related to previous work.

3.1 Selection of sample areas.

The study began in 1968 when a Research Assistant, Miss M.E. Watson, investigated the selection of suitable study sites for work on the population dynamics of some of the rare species in Upper Teesdale. Some sites were established in 1968, the majority in 1969, and a few more in 1970. The sites were situated in closely-grazed turf, or in areas of eroding sugar limestone on Cronkley and Widdybank Fells. They were selected so that records for each species, where possible, could be kept at three different distances from the planned top water mark (TWM) of the Cow Green Reservoir. These distances were A. within 100 metres, B. 200-250 metres, approximately, and C. over 500 metres.

The selection of areas for the location of quadrats was greatly facilitated by maps showing the distribution of rare species on the Fells, prepared by Dr. M.E. Bradshaw with the help of Extra-Mural students. Many of the species studied have very restricted distributions, and the sites had to be selected accordingly.

The sites were grouped into 10 major areas, 9 on Widdybank and one on Cronkley. Doody (1975) gives details of all the sites that were established. Essentially, sites 1, 2 and 3 fell into Group A (above), sites 4, 5, 6 and 7 fell into Group B, and sites

8 (including 8B) and 9 fell into group C. Species were not necessarily represented in each site or in each grouping, depending on their distribution. Details of the quadrats of the species studied are given in chapters 4-7.

Site 10, on Cronkley Fell, was situated on sugar-limestone turf, and some quadrats lay inside originally rabbit-proof enclosures. From about 1972 onwards, rabbit grazing increased considerably within these enclosures, and some of the observed data reflects this.

3.2 Permanent quadrats and sample sites.

Permanent quadrats and sample sites were established once the broad areas for study had been decided. Permanent quadrats were set up to obtain the detailed demographic information that is the basis of this study. These quadrats were all 30cms wide, to facilitate recording without entering the quadrat, and to enable the use of a standard frame, but varied in length from 1 to 5 metres, depending on the density of the plant under study, to ensure the presence of a reasonable-sized sample. These quadrats were marked with inert nylon-coated corner pegs, sunk to ground level so that they were invisible. It was essential for the purposes of the monitoring that the study itself had minimal effects, and therefore the sites had to be apparently identical to the surrounding vegetation as far as sheep, humans, etc., were concerned. The plots were relocated using compass bearings from known landmarks, and eventually by memory, and the system worked well throughout, although one or more corner pegs did gradually become buried.

Much larger, permanently-marked sample sites were set up to provide larger samples of flowers, fruit and seed for the species under study. These were situated as close to the comparable permanent plots as possible, in similar vegetation. Data from these sample sites have only been used where stated, as results from them seemed very inconsistent, and difficult to relate to the behaviour of plants in the permanent quadrats at times. Descriptions of the sample sites are given under the species concerned.

In spring 1973, 2 additional permanent plots and a sample site were established by the author at a site at Cassop Vale, a few miles from Durham City to observe the behaviour of a lowland population of *Primula farinosa* and compare it with the behaviour of the species on Widdybank Fell.

3.3. Definition of individuals in the population has necessarily followed those given by Doody (1975), and are explained for each species in the appropriate chapter. Individuals of *Primula farinosa* were defined simply as plants arising from seed, and this definition worked well in practice.

3.4 Method of recording.

A graduated metal frame, with a movable cross-piece was constructed to the same width as the permanent plots, i.e. 30cms. This frame was placed with 2, or 4 legs, over the marker posts covering the whole quadrat, or one metre of it at a time. For the longer quadrats, a string was lined up at each recording from end to end of the quadrat, and the frame was moved along this, recording each metre consecutively. By placing the frame in the same place on each visit, all known plants could be located easily. Each plant of the species under study was originally located by paired coordinates from the frame, and mapped onto graph paper at 1:10 scale. This was sealed in a polythene bag and covered by a semi-matt drafting film overlay Records of changes, additions, flowers, etc., were then made on to the overlay with reference to the chart below, using waterproof

Mars "lumochrom" pencils of a different colour for each visit. Care was taken to mark the corners of the quadrats on the map so that any movement of the overlay could be adjusted for. This method was adopted so that field records could be made whatever the weather, and it worked well despite the cold, wet and windy nature of the Teesdale climate. Records were made in spring, summer, and autumn, with the exact timing depending on the observed behaviour of the species. The situation at each autumn was then transferred to a new chart, and new overlays prepared for the following season.

The fate of each plant could thus be followed over as long a period as required. The data for all plants was abstracted, with each plant identified by its exact coordinates, and all additions and mortalities defined as appropriate.

The sample sites were recorded for total number of plants of the species, percentage individuals flowering, and counts were made to assess the number of flowers, buds, fruit or seeds per flowering plant as appropriate. Fruits and seeds were collected elsewhere on the Fell for experimental work.

3.5 Data presentation and analysis.

3.5.1 Definitions.

Depletion curve: the survival of a mixed-age population over a period of time (Harper, 1977).

Survivorship curve: the survival of a single-age cohort over a period of time.

Seedling: A seedling is counted as such until after its first winter. Thus, it enters the adult population at 6-12 months old, depending on germination time.

Vegetative addition: non-seedling additions, defined for each species separately.

Seasons: Winter: the 6 month period between about mid-October and mid-April.

Spring: April to July.

Summer: July to the Autumn recording (September/October).

These are arbitrary divisions, but reasonably appropriate to the Teesdale climate.

3.5.2. Problems and assumptions in analysis.

a. The general approach has been to look at each species in two ways; its behaviour overall as represented by the samples taken (i.e. permanent plots) and its behaviour within each sample, or permanent plot. In much of the analysis, therefore, sample size, i.e. the figure for a single site for a given year, is variable and often small, particularly where individual cohorts or groups are being followed. Thus the variance for some of the samples may be great, and difficult to interpret. Some "lumping" has been carried out, therefore, when appropriate, but generally the approach has indicated that there are considerable differences between sites, and they have been kept separate for analysis wherever possible.

b. The commonest variable of which the effect has been studied is time, and time is not random. Samples from a given year may be affected by the previous year in two ways: they include the survivors from the previous year, and their behaviour in a year may be affected by their behaviour in the previous year. The samples therefore are not independent. In general, the problem has been overcome by being ignored, but it is particularly acute where attempts are made to correlate a population variable with conditions in a given year. Flowering, in year _a_, for instance, may depend on the weather in year _a_ at flowering time, during the previous winter, in year _a-1_, or even before that; it will depend on the age structure of the population, which itself reflects the conditions of the past few years; it may depend on flowering in year _a-1_, and other less obvious factors from previous years. The problems have been considered as they have arisen, but should be viewed in the light of these factors.

_c_. The samples (i.e. sites) were originally selected subjectively (Doody, 1975; Bradshaw pers. comm.), and although this need not affect the validity of the analyses _per se_, it becomes impossible to generalise from these sites to the situation on the whole of Widdybank or Cronkley Fell, particularly with regard to population changes. The samples were to some extent selected for their original high density of plants of the study species, compared to other areas where the species occurred, and their most likely short-term future is therefore to decline, (although they need not do so), particularly in the case of shorter-lived species. Both _Polygala amarella_ and _Draba incana_ (recorded but not presented in this thesis) have declined over the period, but this change has to be related to changes in adjacent areas before it can be adequately interpreted.

It has become apparent that the sites are not merely samples of a homogenous vegetation with species populations behaving similarly within them all - in many cases, there is a good deal of evidence that the population samples in some sites behave quite differently, consistently, to other sites in one or more parameters.

d. In general, because of the extreme rarity of the species studied, and the location of the study area within a National Nature Reserve, perturbation and experiment has not been appropriate, despite the likely benefits from such an approach in some cases.

e. Over the longest runs of data used, from 1968-1975, there have been changes in observers. It is assumed throughout that all observed changes are real changes and not facets of different recording techniques. Cross-checks and corrections have been made wherever later evidence is inconsistent with earlier records.

3.5.3 Age specific mortality.

The survivorship of cohorts of known or unknown age was examined for evidence of age-specific mortality for each species. A decision on whether or not mortality is age-independent is critical for the understanding of other observed mortality data. First, the data on the decline of all plants of known-age were pooled and compared for each age-class to investigate the mortality rates between age-classes. It is obvious that there were more data available on the mortality rates of the youngest age-classes, with very little data on the decline of the oldest age-classes, and estimates of their mortality rates was therefore less precise. Pooling of the data in this way was the best method of reducing the overlain effects of different annual conditions, but it assumes that the same pattern of age-dependence is applying in each of the sites, (despite the observed differences in mortality rates). This is indicated in the graphs of Doody (1975) and has not been analysed further. The observed data on age class mortality was then compared with the best estimate of negative exponential mortality (age-independent mortality), using the first and last figures for plant numbers and calculating the appropriate constant mortality rate, by a χ^2 test for goodness-of-fit. The age-specific mortality for each species was thus characterised, and in most cases it was found to approximate to age-independent mortality (but see sections 6.4.1 and 4.4.) In all cases, the mortality was assumed to be sufficiently close to age-independence for further deductions to be made, although the possible inaccuracies resulting from this are discussed in 6.4.1 and Chapter 8.

If mortality is age-independent, and follows a negative exponential pattern, it may be characterised, like radioactive decay, by a half-life. This is a measure of the time taken for half of the population to disappear (excluding additions) and may be calculated using the formula:-

$$\lambda = \frac{\log_e \frac{No}{Nt}}{t} \quad \text{and}$$

$$\text{half-life } \tau = \frac{\log_e 2}{\lambda}$$

where No is the number of individuals at risk, in the original population.

Nt is the number of individuals surviving after time t (in yrs.

λ is a constant for that population.

Half-lives were calculated in this way for mixed-age populations in each plot and subsequent additions over the first 2-3 years, as a useful way of comparing different species or different environmental conditions. All half-lives are calculated using the number of individuals remaining at Autumn 1975, unless the cohort had died out before this. Where appropriate, half-lives were calculated for seedling and vegetative additions separately.

Using the half-life of the mixed-age population, an estimate of the total turnover time of the population may be made, i.e. the time taken for all individuals recorded at a given time to disappear from the population. The "rule-of-thumb" used is that of four times the half-life, and inspection of cohorts or populations that have died out indicates that this estimate is reasonable, or slightly low. It depends, to an extent, on the sample size and the accuracy of the assumption that mortality is totally age-independent. The "total turnover times" quoted are therefore useful comparative estimates, but not accurate predictions. The implicit assumption is that they also give an indication of the greatest age to which individuals can live.

Life expectancies at birth have also been calculated for plants in each quadrat, based on the ages at death of those plants that have died, together with the length of time lived by those surviving. Because the estimates are made for groups of plants where a number are still surviving (rather than a cohort whose individuals have all died out) an assumption has to be made to the effect that the Life Expectancy of the individuals surviving is equivalent to those that have died. In other words, it assumes age-independent mortality, although small departures from this pattern are unlikely to make much difference to the calculated Life Expectancy if several years' records are available. The equation for Le used was therefore:

$$\mathrm{Le} = \frac{\sum n_{x_{1\,\mathrm{to}\,n}} \cdot x_{1\,\mathrm{to}\,n} + n'_{y_{1\,\mathrm{to}\,n}} \cdot y_{1\,\mathrm{to}\,n}}{n_{x_{1\,\mathrm{to}\,n}}}$$

(adapted from Sarukhan and Harper, 1973).

Where Le, the Life Expectancy, is the sum of the number of individuals dying at age x multiplied by x, plus the number of individuals dying at age x', multiplied by x', up to age x_n plus the total of the number of individuals surviving for y years multiplied by y, up to y_n, divided by the number of individuals that die in the period, $n_{x_{1..n}}$ i.e. the individual-years lived by those that have died, plus the individual-years lived by those that have survived, divided by the number dying.

Estimates of half-lives, Life expectancies, and average lengths of life (see section 3.5.4) differ, as expected, since they each measure slightly different aspects of the plant's or the population's longevity. However, in a few cases, one estimate of longevity (e.g. half-life) will indicate that plants in a certain plot are longer-lived than those in a second plot, whilst estimates of, for instance, Life expectancy may indicate the opposite. This may arise because each estimate is based on the mortality of a different section of the population. Half-lives are, generally, based on the mortality of the original mixed-age population; Life expectancies are based on the mortality of plants "born" during the study; and average length of life is based on the mortality of all plants during the period of study, of known or unknown age (although excluding seedlings in some cases). All either assume age-independent mortality, or are most accurate if it occurs.

3.5.4 Annual mortality data.

The apparent mortality of plants in a population may be affected by the way in which the data are presented, and in particular by the time period considered, the inclusion or exclusion of seedlings, and the population that the number of deaths is related to. In most cases, where appropriate, seedlings have been excluded from overall and annual mortality calculations until after their first winter. Although the study has run from Autumn to Autumn, it has been considered advisable in some cases to study mortality over the period Spring-Spring; seedlings from the previous year "enter" the adult population in spring and are therefore "at risk" for only 6 months in their first year as adults if Autumn-Autumn periods are considered, so that their mortality is not strictly comparable with that of the other adults. If they are excluded until the following autumn, it means that they are not considered for the first 15-18 months of their lives, which is a considerable part of the total life-span of many species. It would be possible to include seedlings at their first autumn, and consider the period Autumn-Autumn, but this may give rise to marked fluctuations in mortality that are more a function of the number of seedlings than of any external influences. Where possible, the detail of early seedling mortality is considered separately, and if found to be comparable to that of adults (e.g. in Polygala) they may be considered together. Because data for mortality or survival are binomially distributed, very precise estimates of the variance for individual sites in individual years may be calculated, using the formula:

$$S^2 = \frac{p \cdot q}{n}$$

where p is the proportional mortality
q is the survival (1-p)
and n is the total number of plants at risk (the sample size).

This variance becomes smaller with increasing sample size, and for reasonably large samples (say $n > 100$) the figure obtained for p or q is considered to be very precise, as an estimate of the true P or Q. However, it is not appropriate to use this formula as an estimate of variance of the mean of a number of sites, or the mean of a number of years, as no account would be taken of inter-site or inter-year variation. The means of a series of samples of binomial data usually vary normally, and thus a simple variance for the mean may be calculated by the normal methods; but this does not take into account the inherent precision of the binomial data, and normally gives very wide confidence limits which it is difficult to draw conclusions from.

Hence, it was considered most appropriate to analyse all the data together. A technique similar to analysis of variance was used, but the inherent precision of each sample figure allowed a χ^2 to be calculated for each source of variation, with a correspondingly more sensitive distinction being made between sites or between years.* Further, the "Residual variation" calculated as in an analysis of variance could be treated as an estimate of the degree of interaction between sites and years, and the probability of the calculated degree of interaction occurring could be estimated "Interaction" between sites and years is caused by some sites reacting differently to other sites in a given year, not in the degree of their reaction but in its direction. In other words 1972 conditions might depress mortality in 4 sites but raise it in 2; 1973 might then depress it in the 2 sites where it was raised in 1972, and the other 4 sites might be raised. Normally the difference is not that clear-cut, but if the degree of interaction is high, it serves as a reminder that the sites may respond to the same environmental conditions quite differently. This analysis reveals the presence or absence of significant differences between years, or between sites, but it does not indicate the exact source

* See over

* This was calculated, after normal analysis of variance, using the following equation, taking Years x Sites mortality analysis as an example:

$$\chi^2 = \frac{\text{Year Sum of Squares}}{\text{Pure error}}$$

where the degrees of freedom =(No. of years - 1). χ^2 values could be calculated in a similar fashion for sites, or sites x years. This test was used in a similar fashion to the Variance Ratio test, where appropriate but it is more sensitive.

of the variation. The initial analysis was therefore followed by partition of the data and re-analysis, after inspection to determine the likely causes of the differences. Thus the contribution of any one year or any one site could be determined, although this was not necessarily clear-cut. Probabilities have been assigned to particular years or sites on the basis of their contribution to the overall significance of the differences in the data. Unlike some methods of analysis, this particular method takes into account the differing sample sizes used which are so difficult to avoid in long-term population analyses. The comments about the inter-dependence of year samples made in 3.5.2(b) must still apply, however.

On the basis of the overall average annual mortality of all plants, average lengths of life for plants have been calculated using the formula:-

Dunnet et al (1963)

$$\text{Ave. length of life} = \frac{2-M}{2M} \quad \text{where } M = \text{the proportional annual mortality.}$$

3.5.5 Seasonal mortality data.

Records of changes in numbers were taken three times each year at comparable times, so it is possible to compare mortality rates over each of the three periods of the year. The winter period is 6 months while the 2 summer periods are each 3 months. The mortality during the winter period is adjusted therefore by using the formula:-

$$M_{3\text{months}} = 1 - \sqrt{1-M_{6\text{months}}}$$

Comparisons were then made by a χ^2 test on the mortality rates for each period.

3.5.6 Recruitment.

Recruitment by seedlings or vegetative means has been treated in the same way for the purposes of numerical analysis. Recruitment is quoted as a rate per plant in the population at a given time of the year, at the period when most recruitment takes place, e.g. Seedling recruitment for Viola rupestris is the number of seedlings per adult in the population at the spring record.

Analysis of the recruitment data has been made using a two-way analysis of variance, where Time is the Treatment and sites are the Blocks. This gave an indication of the likelihood of differences being present between years or between sites. Recruitment data are not, of course, binomial and the initial significance of the data was assessed using the normal variance ratio test. Hence if variation between sites and years is too high, differences will not be distinguished. Individual differences were assessed using a Least Significant Difference Test, or a Least Significant Ratio test.

It is not strictly appropriate to compare any pairs of means using the LSD test because the probability of making a Type 1 statistical error increases with the number of means, and normally only the most widely different means were compared. Where appropriate, seasonal differences in recruitment were analysed using a χ^2 test.

3.5.7 Reproductive data.

Distribution of ages at first flowering and comparable data were calculated using only plants from the earliest two years of the study, to avoid bias towards the younger flowerers, although the total sample was not very large.

Analysis of flowering percentage was made using standard analysis of variance techniques, except that proportional data were used, transformed according to $\sqrt{p}$ or $\sqrt{p + 0.5}$ depending on the range of the figures. Further analysis was carried out as for recruitment data.

Percentage flowering was simply the percentage of the total plants in the population that produced flowers of some sort, in a given year.

Numbers of buds, flowers and ripe capsules produced were counted in the permanent plots. Samples (normally 30) of capsules or other fruit, as appropriate, were collected from sample sites and the average numbers of seeds per fruit calculated. To obtain an estimate of the number of seeds produced per plant in the permanent plot, the observed number of capsules was multiplied by the average number of seeds per capsule calculated from the nearest sample, and divided into the number of plants present (usually expressed as seeds per 100 plants). It was assumed that the number of seeds per capsule from the sample site was equivalent to that in the permanent plot; in general differences between sites were not large, and the error is likely to be small. It is possible that capsules matured and were broken off, e.g. by sheep, between visits, although the error from this source is likely to be slight. Frequent visits were made during the flowering season, and remains of naturally-dispersed capsules were visible, and an estimate of the state of a capsule that had been removed could be made from its remaining stalk.

Chapter Four

Polygala amarella

4.1 Introduction.

Polygala amarella (Fearn 1975)(formerly P. amara)* is a small rosulate perennial, occurring in only a few isolated localities in the British Isles. It is listed as a rare species within the British Isles (Perring and Farrell, 1977), occurring in only 13 10 Km. squares, and its population in Teesdale, one of its 4 disjunct areas of distribution, was estimated at c. 1500-2000 plants in 1970 (Bradshaw and Doody, in press). Within Teesdale, it occurs on Cronkley Fell as separate blue-flowered and pink-flowered populations, and on Widdybank Fell as a population of entirely blue-flowered plants, re-discovered in 1957 (Fearn, 1971). Plants from each of the main areas of distribution in the British Isles show persistent morphological differences, suggesting a reasonably long period of isolation, although the variants are not considered to warrant separate varietal status. The Teesdale plants show floral characteristics most similar to those of Scandinavian material (Fearn, 1971, 1975).

For the purposes of this study, the "unit of reproduction" and the units of the populations were considered as single individuals arising from seed. Basal branching may occur, but these branches remain clearly attached to the main stem, and are therefore simply treated as part of the individual. Reproduction over the whole study period was entirely from seed. P. amarella is considered as one of the plants of the "Teesdale assemblage"

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* Fearn, 1971, showed that the British populations of Polygala amara agreed closely, on morphological grounds, with P. amarella, and she changed the name accordingly.

of rare plants, and presumed to have survived in the area since the end of the last Ice Age, although there is no sub-fossil evidence of this species in Post-Glacial deposits, (Fearn, 1975), possibly because its populations have always remained small.

Today, the populations in Teesdale are undoubtedly sufficiently small to be considered to be in danger of extinction, particularly in view of the findings of the present study, which has shown that, in most years, more plants die than are recruited into the population.

4.2 The recording sites.

Five permanent quadrats were established as described in 3.2., four on Widdybank Fell and one on Cronkley Fell. Those on Widdybank contained only blue-flowered plants and that on Cronkley contained only the genetically-different pink-flowered plants, although limited records were made on the Cronkley blue-flowered population without permanent quadrats. The Widdybank quadrats were all established at about 200-250 metres from the top water mark of the reservoir, because of the localised distribution of Polygala on this Fell.

Quadrat 6:1 lay on a west-facing slope in sheep-grazed grassland, dominated largely by Festuca ovina and Sesleria, with smaller amounts of Kobresia simpliciuscula, Helianthemum chamaecistus, Briza media, and two species whose populations were recorded - Viola riviniana and Potentilla crantzii.

7:1 was dominated by Festuca ovina and Sesleria, but the sugar-limestone turf graded into patchy Calluna. Kobresia simpliciuscula was present in reasonable quantities, and Plantago maritima, Antennaria dioica, Gentiana verna and Briza media were also present. Doody (1975) shows a map of one metre of this quadrat.

7:2 lay quite close to 7:1, but differed in the absence of Calluna and Kobresia simpliciuscula and in its closer proximity to eroding exposed sugar limestone. It was also recorded for Gentiana verna. "Draba stone" (Qu. 7:3 in Doody, 1975) was unusual in that the Polygala plants were growing in a loose moss/ lichen layer overlaying limestone rock. Much of the quadrat was bare rock, and those parts lying to either side of the rock were largely dominated by Calluna. Draba incana was also recorded, although the results are not presented here.

Black Ark on Cronkley Fell lay in a rabbit- and sheep-grazed grassland/dwarf shrub area. Festuca ovina and Sesleria dominated parts of this quadrat, although in other parts Calluna and Empetrum nigrum were dominant. Parts had a close "turf" of lichens, especially Cladonia spp.

Sample sites Two sample sites were set up on Widdybank Fell, close to quadrats 7:1 and 7:2, and one on Cronkley Fell immediately adjacent to the permanent quadrat, in which pink-flowered plants were recorded. The population was considered to be too small to risk collection of fruit and seed samples.

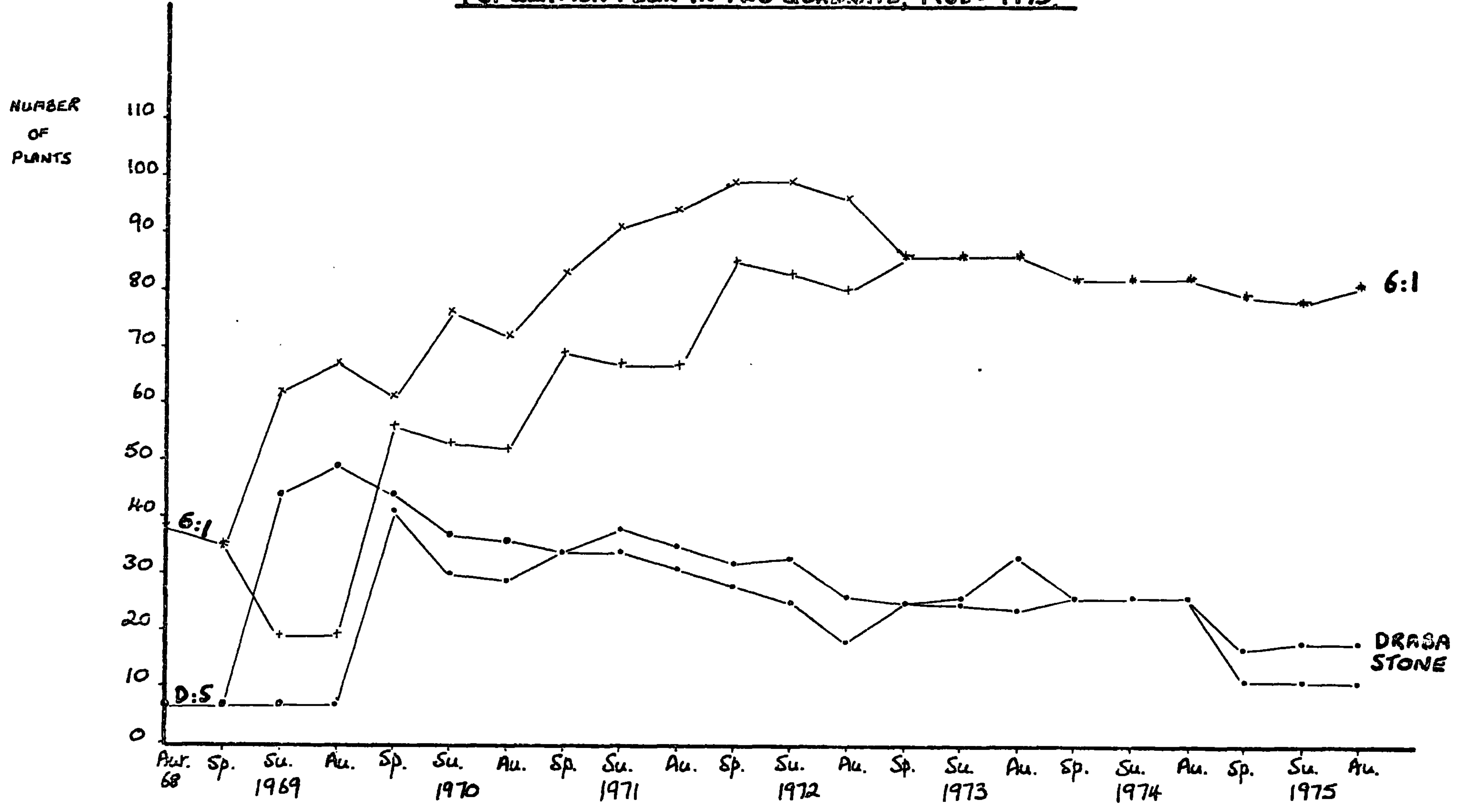
4.3 Population flux.

The populations of Polygala amarella have been recorded since Autumn 1968. From the seven years of data available, a general pattern that is shown by the total population and all individual quadrats (except 6:1) is that of a general more or less constant decline in numbers since the peak of numbers in Summer-Autumn 1969. This 1969 peak was considerably higher than the initial 1968 levels, and overall the total numbers of plants recorded was about the same in 1975 as in 1968 (See Figs. 4.1, 4.2 and 4.3). The population sample of pink-flowered plants on Cronkley showed very similar behaviour over the period.

FIG 4.1.

POLYGALA AMARELLA

POPULATION FLUX IN TWO QUADRATS, 1968 – 1975.



LOWER TOTAL FOR EACH QUADRAT IS TOTAL MINUS SEEDLINGS

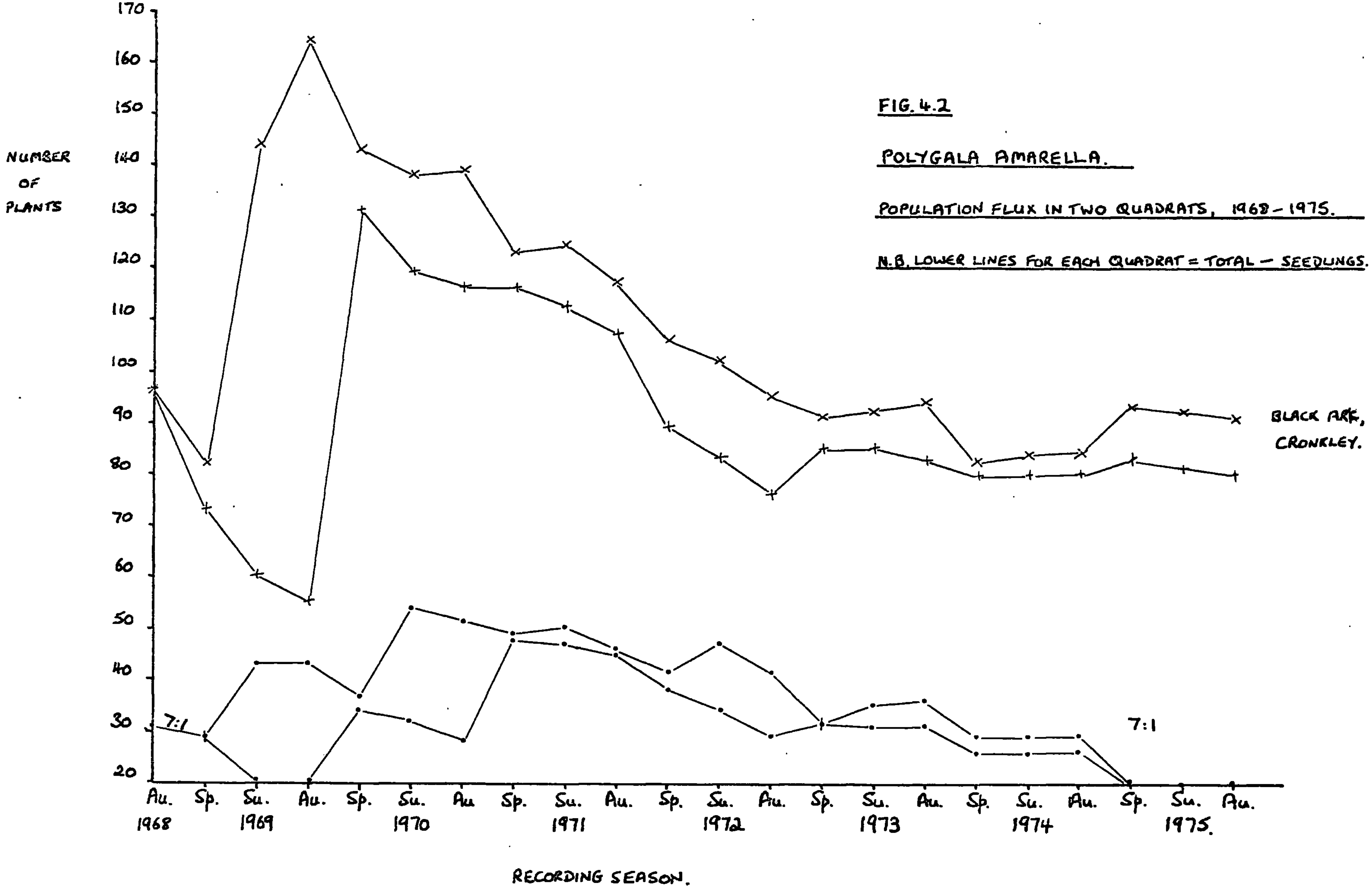


FIG. 4.2

POLYGALA AMARELLA.

POPULATION FLUX IN TWO QUADRATS, 1968 – 1975.

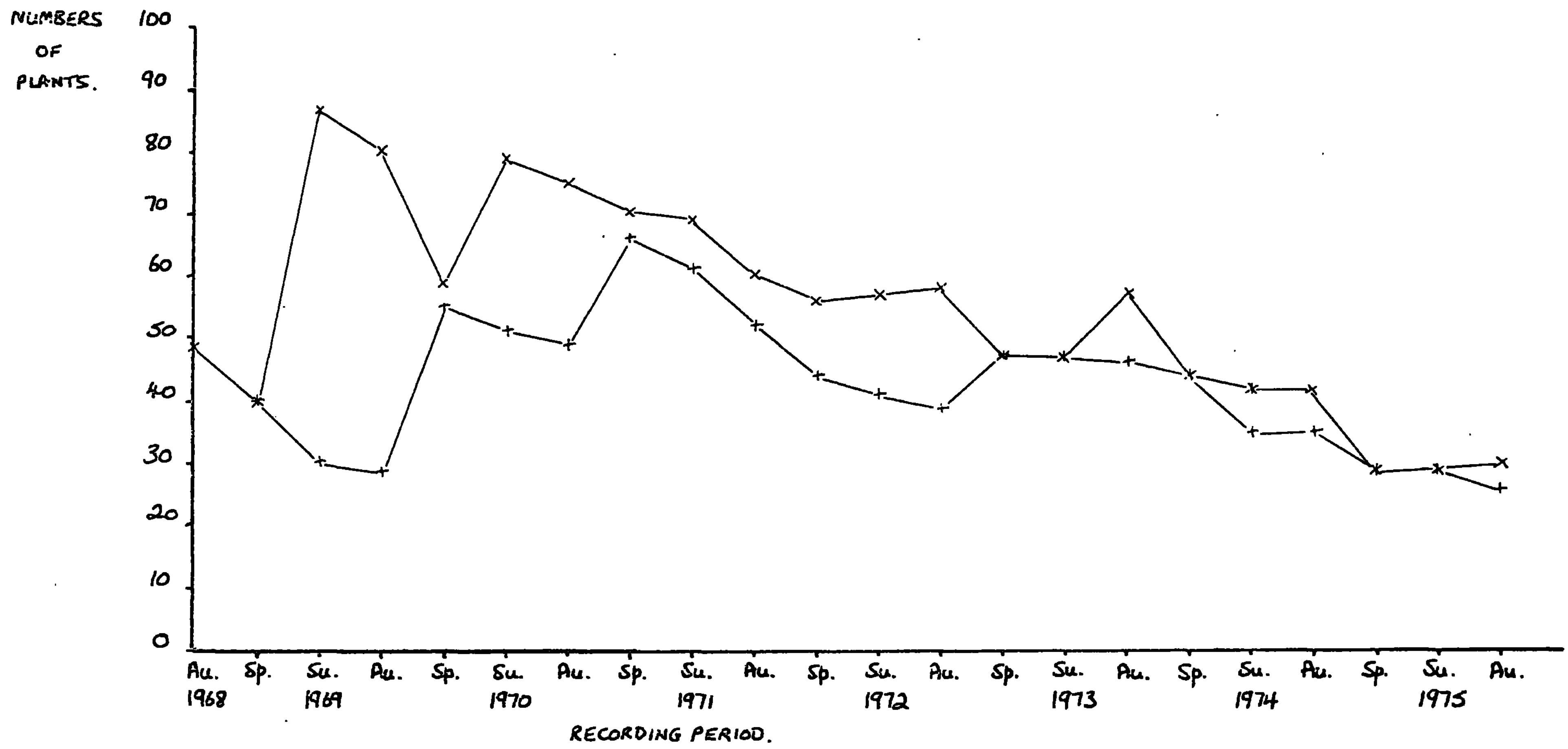
N.B. LOWER LINES FOR EACH QUADRAT = TOTAL – SEEDLINGS.

FIG. 4.3

POLYGALA AMARELLA

POPULATION FLUX IN 7:2, 1968-1975.

LOWER LINE REPRESENTS TOTAL - SEEDLINGS.



Reference to Table 4:1 reveals the mechanics of these changes. 1969 was an exceptionally good year for seedling establishment, with a total of 300 seedlings recorded in quadrats during the year. For comparison, in the second best year (1970) only 113 seedlings were recorded. Mortalities were highest in 1969 and 1970, and the pattern since then has been a general excess of mortalities over additions, with the consequent steady decline in numbers.

A longer period of recording is required before the full mechanics of the changes in numbers can be understood. In all years except one, mortalities have exceeded additions. If this pattern is reasonably typical, and good seedling years do not occur very frequently, then clearly the population will decline. From the available evidence, it would appear that Polygala amarella needs a very good seedling year at least once in every 6-7 years to maintain its populations, assuming that its performance over the period 1968-1975 was reasonably typical.

The calculated average length of life of Polygala amarella in these sites is 3.65 years (see Table 4.5), and the calculated Life expectancy of individuals at birth is 4.47 years (see Table 4.4.). The population is unlikely, therefore, to persist long without recruitment.

Although there are considerable seasonal differences in numbers, these follow no particular pattern, such that the lowest number of plants may be recorded in any season. Over the 7 year period, additions are significantly higher than average ($P < 0.001$) per period of time, in the summer (between the May and July recordings), and significantly lower ($P < 0.001$) in the other periods. This agrees with the general observation that most

Polygala amarella

Table 4.1

Separate additions and mortalities in all permanent plots

Season	Seedling additions	Mortalities	Change in pop. nos.	Pop. nos. incl. all seedlings
Aut. 1968				221
Spr. 1969	9	37	-28	193
Sum. "	240	53	+187	380
Aut. "	51	28	+23	403
Spr. 1970	26	86	-60	343
Sum. "	78	37	+41	384
Aut. "	9	20	-11	373
Spr. 1971	26	40	-14	359
Sum. "	25	12	+13	372
Aut. "	6	26	-20	352
Spr. 1972	50	68	-18	334
Sum. "	22	18	+4	338
Aut. "	5	27	-22	316
Spr. 1973	6	42	-36	280
Sum. "	6	0	+6	286
Aut. "	24	4	+20	306
Spr. 1974	18	61	-43	263
Sum. "	9	9	0	263
Aut. "	0	0	0	263
Spr. 1975	22	48	-26	237
Sum. "	4	6	-2	235
Aut. "	7	5	+2	237

seedlings appear in the early summer. Mortalities are significantly higher than average ($P < 0.001$) per month during the winter period (October-May), and significantly lower than average ($P < 0.001$) in the late summer-autumn period (July-September/October). Although mortalities in summer (May-July) tend to be lower than average (in 5 out of 7 years) the difference is not significant. This contrasts with the findings of Doody (1975) that plants were more likely to die in the summer period (6 months), although it is noticeable that this distinction was not present towards the end of his recording period, 1968-1972.

4.4 Mortality rates and Life expectancies.

In general, about 1/3 to 1/4 of the plants of Polygala in the permanent plots died each year. Considerable variation existed between sites and between years, and different analyses of the data could exaggerate or lessen these differences.

4.4.1 Age specific mortality.

Table 4.2 directly compares the survival of equivalent age classes in different years. In attempting to assess the effect of age on mortality, it should be noted that this study has not continued long enough to allow comparable sized samples to be observed for all age classes. Only relatively small numbers of plants have been followed from 4 to 6 years of age, and the data becomes correspondingly more prone to random fluctuations for these older age groups. In addition, it is not possible to completely separate the effects of age from those of the year (weather etc.) although the same age classes are compared from different years.

The analysis presented in Table 4.2 suggests that mortality is more or less age-independent, although mortality from 3 to 4 years is significantly lower ($P < 0.001$) than the overall average. Mortality of plants of this age was 0.136, compared to the

Polygala amarella

Table 4.2

Year class survival : Age classes compared.

Year first recorded	Period of survival in years. Autumn figures							
	Total seedlings rec.	No.at first Aut. (0)	1	2	3	4	5	6
1969	300	274	185	148	99	89	68	54
1970	113	99	80	57	49	39	27	
1971	57	50	39	34	29	25		
1972	77	74	62	39	28			
1973	36	36	33	23				
1974	27	27	24					
1975	33	33						
Totals in ea. class	643	593	423	301	205	153	95	54
Prop. surviving		0.922	0.755	0.754	0.737	0.864	0.742	0.794
Mortality		0.078	0.245	0.246	0.263	0.136	0.258	0.206
Whether significantly diff. from mean			NS	NS	NS	$P<0.001$ Higher	NS	NS

average of 0.241. No convincing explanation for this pattern can be adduced, (although it is also the age at which most plants first flower) and further work is required to test its validity. The age groups of 4-5 years and 5-6 years show mortality rates that are not significantly different from the mean. Seedling mortality, when adjusted for the length of time the seedlings had been recorded (either 3 months or 6 months), is 0.258 p.a. which is not significantly different from average. In summary, therefore, mortality is age-independent from time of germination and through all age-classes up to 7 years with the apparent exception of the 3-4 year age group which exhibits a significantly lower mortality. On the basis that mortality is more or less independent of age (ignoring the apparently reduced mortality at 3-4 years), it is reasonable to calculate half-lives by analogy with radioactive decay rates, as discussed in Section 3.5. For Polygala amarella, the half-lives of the original 1968 mixed age populations vary from 1.41 years to 8.66 years, depending on the site (see Table 4.3). In addition, there is considerable variation between the different age cohorts analysed up to summer 1971, although in no case is there any statistical significance in the differential survival rates of different cohorts. It is immediately apparent that plants survive considerably better in site 6:1, on Widdybank Fell, with half-lives above average in every case, and these differences are significant ($P < 0.001$). Survival rates in Black Ark (Cronkley, Pink flowered) are also significantly higher than average, whilst those in 7:1 (Widdybank) are lower. These inter site differences are discussed in detail below, under section 4.7.4. Using the "rule of thumb" that the total turnover of plants will normally take place in a period of about 4 times the calculated half-life

Polygala amarella

Table 4.3

Half-lives of mixed-age populations and age cohorts (in yrs)

	6:1	7:2	7:1	Draba stone	Black ark	Widdybank sites (blue)
Mixed-age pop. Aut.'68-Aut.'75	8.66	1.51	1.41	3.30	2.24	2.04
Spring 1969 additions	NR	NR	NR	NR	2.04	NR
Summer 1969 additions	5.33	1.93	1.31	1.65	3.01	2.31
Autumn 1969 additions	2.57	1.93	0.50	1.98	2.89	2.17
Spring 1970 additions	4.07	1.98	1.50	2.04	2.77	1.98
Summer 1970 additions	5.33	1.69	1.87	1.65	4.33	2.31
Autumn 1970 additions	NR	NR	NR	NR	6.30	NR
Spring 1971 additions	4.62	1.51	No deaths	NR	3.47	3.15
Summer 1971 additions	5.78	1.12	NR	4.33	5.33	3.15

Polygala amarella

Table 4.4

Life expectancies for plants in each quadrat

Quadrat	Calculated life expectancy for known-age plants recorded from 1969 - 1975 (years)
6:1	8.05
7:2	2.86
7:1	3.55
Draba stone	3.36
Black art	5.24
All plants	4.47

(see section 3.5), we can estimate the turnover time for plants in site 6:1 to be in the region of 25-30 years, 5-6 years in site 7:1, 10-14 years for plants at Black Ark, Cronkley, and 8-10 years overall for the sites on Widdybank Fell.

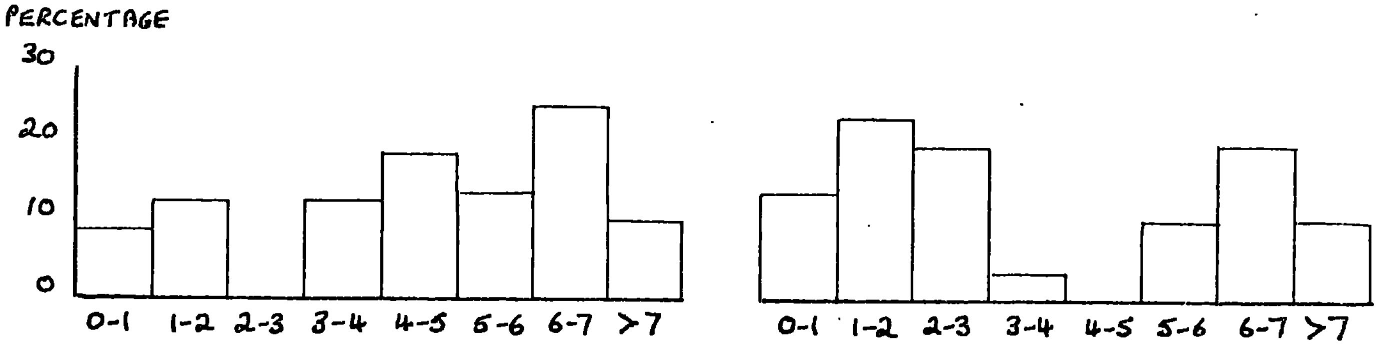
Life expectancy values for plants at birth have been calculated for each quadrat, as explained in Section 3.5.3 (see Table 4.4). These values confirm the suggestion that plants in 6:1 and Black Arc have a greater length of life than plants in other quadrats). For all plants in all quadrats, the calculated average length of life, based on the formula $\frac{2-M}{2M}$ is 3.65 years (see Table 4.5).

4.4.2 Age structure of the population.

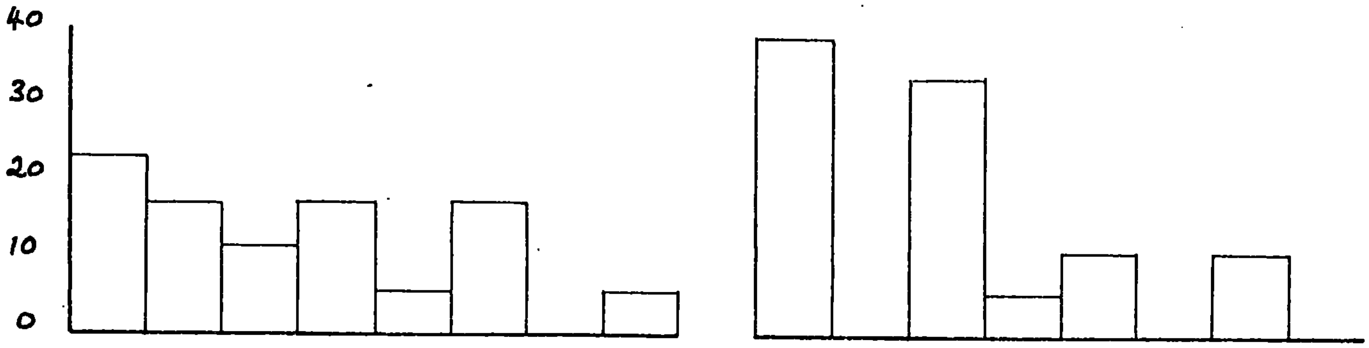
The age structure of a population reflects the annual mortality and recruitment rates over the period during which it was formed. Since Polygala amarella is a relatively short-lived perennial, a high proportion (c. 90%) of the plants in the permanent quadrats were of known-age at Autumn 1975, and reasonably accurate age class distributions could be calculated for each site, as shown in Fig. 4.4. Particular features of interest are shown by the Draba Stone site, where the whole population is of known-age, reflecting the slightly higher mortality rate at that site; and the relatively high proportion (67%) of plants in 6:1 that are over 4 years old, reflecting the lower mortality and higher longevity figures recorded for that site. The higher percentage of plants than expected in the 6-7 year class is a reflection of the exceptionally high recruitment in 1969, which skews the distribution towards the older age classes. A "model" age-class distribution for a population with 25% mortality and constant recruitment is presented for comparison, with which none of the populations is very similar.

FIG. 4.4. POLYGALA AMARELLA

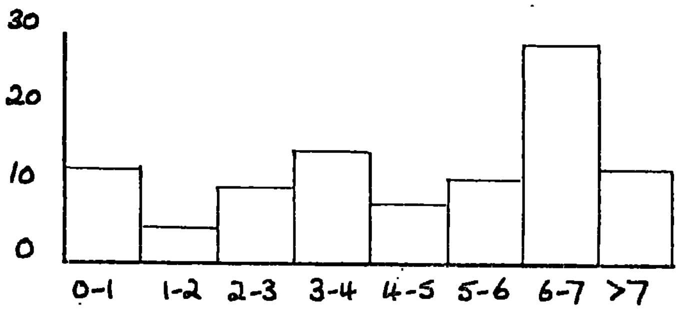
AGE CLASS DISTRIBUTIONS. AUTUMN 1975.



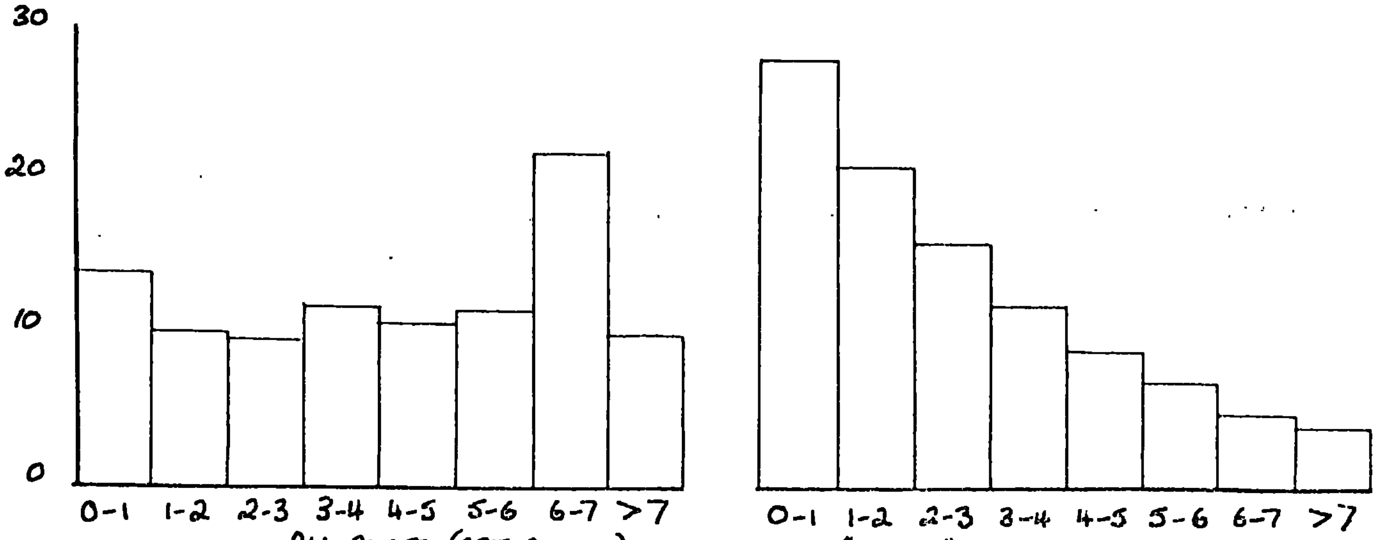
6:1 (81 PLANTS) 7:2 (30 PLANTS)



7:1 (17 PLANTS) DRABA STONE (18 PLANTS)



BLACK ARK (91 PLANTS)



ALL PLOTS (237 PLANTS) "MODEL" POPULATION 25% MORTALITY.

4.4.3 Annual mortality rates.

Considerable differences may exist between apparent annual mortality rates according to the method of analysis, as discussed in Section 3.5.4., although it is clear that there are certain underlying trends. Table 4.5 compares the annual mortality of all plants in all plots together, using Autumn records only, and comparing the changes between one Autumn and the next relative to the number of plants present at the start of each interval. The mortality of seedlings during their first spring and summer is therefore excluded, but mortality over their first winter is included, and any seedlings present at the Autumn record are included in the population total. With these provisos in mind, it was found that the overall mortality rate was 0.241 per annum (i.e. on average 24% of plants die each year), and that mortality rates were significantly higher than average in 1969-1970 (0.320) and 1971-1972 (0.312), but significantly lower in 1970-1971 (0.190) and 1972-1973 (0.146). Mortality in 1973-1974 and 1974-1975 was not significantly different from average. The overall amplitude of these average values is 0.174, from 0.320 to 0.146.

Table 4.6 compares annual mortality in each site over the period 1969-1975 using spring records. Seedlings are excluded from the calculations until after their first winter. Analysis of variance fails to detect any consistently significant differences between years or between sites, but the more sensitive test using χ^2, as discussed in Section 3.5.4, indicates that differences do exist. Overall, the indication is that there is significant difference in mortality rates between the sites, and between years, ($P < 0.001$ in each case) but that there is apparently no interaction between years and sites, i.e. different sites do not appear to react differently to different years. Further separation

Polygala amarella

Table 4.5

Year class survival : Years compared.

Year first recorded	Period of survival. Autumn figures.						
	1969	1970	1971	1972	1973	1974	1975
1969 original pop.	129	89	74	47	36	28	23
1969	274	185	148	99	89	68	54
1970		99	80	57	49	39	27
1971			50	39	34	29	25
1972				74	62	39	28
1973					36	33	23
1974						27	24
1975							33
Totals	403	373	352	316	306	263	237
Propn. surviving.		0.680	0.810	0.688	0.854	0.771	0.776
Annual mortality		0.320	0.190	0.312	0.146	0.229	0.224
Whether significantly diff. from av.		P<0.001 L	P<0.01 H	P<0.01 L	<0.001 H	NS	NS

Mean proportion surviving $\frac{1528}{2013} = 0.759$

Mean mortality $= 0.241$

Mean length of life $\frac{(2-M)}{(2M)} = \frac{1.759}{0.482} = 3.65$ yrs.

Polygala amarella

Table 4.6

Annual mortality 1969-1975, spring-spring.

Years	Sites					
	6:1	7:2	7:1	Draba Stone	Widdybank Averages	Black Ark
Spr. 69-Spr. 70	0.57	0.43	0.41	0.29	± 0.20 0.46	0.47±0.05
Spr. 70-Spr. 71	0.13	0.24	0.26	0.34	± 0.16 0.23	0.25±0.04
Spr. 71-Spr. 72	0.10	0.41	0.23	0.26	± 0.22 0.25	0.32±0.04
Spr. 72-Spr. 73	0.15	0.27	0.39	0.39	± 0.20 0.26	0.24±0.05
Spr. 73-Spr. 74	0.20	0.26	0.32	0.32	± 0.10 0.25	0.18±0.04
Spr. 74-Spr. 75	0.06	0.50	0.46	0.58	± 0.39 0.32	0.01±0.01
Site averages	0.17	0.35	0.33	0.37	± 0.16 0.28	0.25
	±0.33	±0.19	±0.16	±0.21		±0.27

Mortality here is calculated excluding seedlings until after their first winter, and related to the adult population at the start of each period.

N.B. In "Widdybank Averages" column, lower figure is the average.

of the data, after inspection, indicates that the source of the variation between sites arises almost entirely from plants in 6:1. Mortality in this plot is significantly different to all others ($P < 0.001$), whereas, when this plot is excluded, there is no significant difference between the other plots, and - in fact - virtually no difference at all. Similarly, further separation of the data indicated that the period Spring 1969 - Spring 1970 had a very different rate of mortality ($P < 0.001$) compared to all other years, and that when this was removed from the data, there was no significant difference between the other years. The difference between site 6:1 and the remaining sites persisted whether 1969-1970 was considered or not.

In summary, therefore, it can be concluded that:-

1. There was no significant annual variation in mortality over the period 1969-1975 except for the period from Spring 1969 - Spring 1970, where mortality was considerably and significantly higher than average.

2. Site 6:1 shows consistently and significantly lower mortality rates than all other plots, amongst which no significant differences can be detected. This is reflected in the longer half-life and greater Life Expectancies of the population in this quadrat, and its significance is discussed below, in 4.7.4.

3. That there are no conclusive grounds for believing that plants in different plots react differently to each other with regard to the conditions in any given year. This does not mean that no such difference exists, but simply that it is not possible to distinguish any such effect from the data. The reasons for such annual differences as exist, and the possible significance of the suggestion that the plants in all sites react in a similar fashion to a given set of annual conditions, are discussed further, with reference to other species, in

Chapters 8 and 9.

4.4.4 Seasonal mortality patterns.

To attempt to understand the factors underlying the mortality of plants of Polygala, or any species, it is useful to discover the period of the year in which maximum mortality takes place, if any. Doody (1975) found that there was no significant recurring differences between the specific survival rates in any particular season for this species, over the period 1968-1972. However, as indicated under Population Flux (section 4.3), there is evidence that mortality per unit time is greater during the winter months over the whole period 1968-1975. Table 4.7 shows the detailed records of mortality in all plots for each season over the period Autumn 1972 - Autumn 1975. The mortality figures are calculated as the number of plants dying in the period related to the number of plants at risk at the start of the period, excluding seedlings until after their first winter. Analysis of Table 4.7 indicates that mortality per period of time is considerably higher in winter than in either of the other 2 seasons ($P < 0.001$).

4.5 Recruitment.

4.5.1 Seedling recruitment rates.

Polygala amarella reproduces entirely by seed, and since 25% or more of the adult plants die each year, the rate of germination and establishment of seedlings is of great significance to the species survival. Table 4.8 shows the annual rate of recruitment for each site for the period 1973-1975. Doody (1975) presents comparable figures for the period 1969-1972, and his average values for each site and year are shown below for comparison:-

Polygala amarella

Table 4.7

Seasonal mortality.

Season	Sites					
	6:1	7:2	7:1	Draba Stone	Black Ark	Averages
Autumn 1972						
Spring 1973	0.07	0.12	0.19	0.03	0.07	0.09
Summer "	0.00	0.00	0.00	0.00	0.00	0.00
Autumn "	0.00	0.02	0.00	0.04	0.02	0.01
Spring 1974	0.11	0.15	0.18	0.15	0.09	0.12
Summer "	0.00	0.26	0.00	0.00	0.00	0.04
Autumn "	0.00	0.00	0.00	0.00	0.00	0.00
Spring 1975	0.05	0.26	0.27	0.35	0.01	0.10
Summer "	0.01	0.00	0.18	0.00	0.02	0.03
Autumn "	0.00	0.12	0.07	0.00	0.01	0.02
Site Aves. 1972-1975	0.04	0.11	0.12	0.10	0.03	0.06

1969	2.22	6:1	0.51
1970	0.40	7:2	0.67
1971	0.17	7:1	0.50
1972	0.27	Dr. Stone	0.69
		Black Ark	0.47

It is obvious that 1969 was the best year for seedling recruitment, in our sites, by a factor of over 5 times that of the next most successful year (1970). Seedling recruitment over the period 1971-1975 has been,relatively, extremely poor. Analysis of Table 4.8 indicates that there are no significant differences either between sites or between years in recruitment values for the period 1972-1975. Preliminary inspection of Table C in Doody without reference to sample size, suggests that there were no differences between sites over the period 1968-1972, though annual differences were observed, as described.

In the period 1972-1975, on average, recruitment in all sites or in all years was below the average mortality rate for the period (0.24), and was only occasionally exceeded by records for individual quadrats in a given year. All plots showed a decline in total numbers of plants in the populations over this period and it is apparent that occasional good seedling establishment years are vital for the persistence of the species. If recruitment persisted at the average 1972-1975 level at barely half that of the mortality rate, the population would die out completely in 25-30 years.

In a preliminary attempt to understand the mechanics of the period between seed dispersal and seedling establishment, and following the suggestion of Doody 1975 that seed germinates within a year after dispersal, a comparison between the amount of seed produced in one year with the number of seedlings recorded in the following year was attempted, see Table 4.9 below.

Polygala amarella

Table 4.8

Annual recruitment of seedlings.

Year	Sites					
	6:1	7:2	7:1	Draba Stone	Black Ark	Aves.
1973	0/86 0.00	11/47 0.23	5/31 0.16	9/25 0.36	11/85 0.13	36/274 0.13
1974	13/69 0.19	7/35 0.20	3/26 0.12	0/26 0.0	4/80 0.05	27/236 0.11
1975	7/74 0.09	4/29 0.14	4/14 0.29	7/11 0.64	11/81 0.14	33/209 0.16
Averages	20/229 0.09	22/111 0.20	12/71 0.17	16/62 0.26	26/246 0.11	96/719 0.13

The figures give number of seedlings per adult plant in the population at the summer recording for that year.

Table 4.9

Comparison between number of seeds produced in one year with the number of seedlings recorded the following year. Widdybank Fell plots.

Seeds per 100 plants in year n, (Estimated). a.		Seedlings in yr. (n + 1) per 100 plants in yr. n. b.	b/a
1969	323	88	0.27
1970	303	22	0.07
1971	264	23	0.09
1972	224	14	0.06
1973	120	23	0.10
1974	111	14	0.13
1975	48	22	0.46
Totals	1393	188	0.12 *

* calculated from the original numbers of seeds and plants, and not as the mean of $^b/_a$.

Preliminary inspection of the ratios, and use of a simple scatter diagram indicates that there is no correlation at all between these two variables. It is of interest to note that, on average 12 seedlings germinate for every 100 seeds dispersed, although this estimate should be treated with a degree of caution on account of the errors implicit in its calculation (See section 3.5.6).

4.6 Reproductive performance.

4.6.1 Age at first flowering and length of reproductive life.

During the period of study, Polygala amarella plants reproduced entirely by seed, and, therefore, the age at which plants may first flower, and the number of times that they can flower are critical factors, in addition to the amount and viability of the seed produced after flowering. Table 4.10 indicates the distribution of the ages of plants at their first flowering,

Polygala amarella

Table 4.10

Length of life and flowering performance.

a) Ages of plants at first flowering.

Age group (yrs)	Numbers and percentages (in brackets) of plants in each age group.		
	Cronkley	Widdybank	Overall
0-1	1 (4%)	0 (0)	1 (2)
1-2	5 (19)	3 (11)	8 (15)
2-3	8 (31)	8 (30)	16 (30)
3-4	11 (42)	13 (48)	24 (45)
4-5	1 (4)	3 (11)	4 (8)
5-6	0 (0)	0 (0)	0 (0)

b) Length of time plants have been recorded without flowering.

	Cronkley	Widdybank	Overall
Number recorded for over 5 years without flowering, from birth.	0	0	0
Number recorded for over 5 years without flowering, from original population.	6	2	8
Number recorded for over 4 yrs. without flowering, from birth.	22	42	64

using the data from the first two years' recording only, to avoid bias as explained in Section 3.5.7. From this, it is apparent that one plant has been recorded as flowering in its first year, on Cronkley Fell (although this may be a recording error) and that increasing percentages are recorded in subsequent age classes until a peak of numbers is reached at 3-4 years. A small number (8%) flower first at 4-5 years, and none are recorded flowering at 5-6 years for the first time.

No plants have been recorded for over 5 years, from birth, without flowering, although a few of the original mixed-age population of plants (which may have flowered before 1968) have persisted for over 5 years without flowering (see Table 4.10). The sample size of plants of this age is too small for firm conclusions to be drawn.

Polygala amarella is not monocarpic in the study area, and, as Table 4.11 shows, may regularly flower more than once. One plant, on Widdybank, has been recorded flowering five times, and although the short period of recording has made the observation of many such examples unlikely, it is probable that very few individuals flower so many times, in view of the short average length of life of Polygala, and the fact that only one plant was observed flowering four times.

4.6.2 Effect of flower production on survival of individuals. Overall, 32% of plants die within their year of first flowering, the remaining 68% surviving either to flower again or die in a subsequent year. The average annual mortality of Polygala plants is about 25%, so, although flowering may slightly increase the risk of mortality, the sample is not large enough to be sure that it is a real effect. It might be expected a priori that a plant that flowered and set seed would be at greater risk, from

Polygala amarella

Table 4.11

Flowering performance

	(Pink) Cronkley	(Blue) Widdybank	Overall
Percentage of plants dying within the year of first flowering	43	22	32
Percentage of plants that flower and survive to a further year	57	78	68
Number of plants flowering twice	7	21	28
Number of plants flowering three times	0	12	12
Number of plants flowering four times	0	1	1
Number of plants flowering five times	0	1	1

depletion of resources, increased chance of accidental uprooting, etc., than a non-flowering plant. The proportion of plants in the Cronkley population that die within their year of first flowering is considerably higher, at 43%, than the average Widdybank figure (22%), which is very comparable with the records from Gentiana (45%), although the reason for this higher mortality on Cronkley is not clear but is perhaps associated somehow with rabbit-grazing. Further, no plants on Cronkley Fell flowered more than twice.

4.6.3 Flower, fruit and seed production.

Plants normally begin to flower in the second or third week of May, and produce indeterminate inflorescences that may persist through the summer until the first frosts. Seed may be set from any of these flowers, but later ones frequently fail to set seed, and the buds around the tip of the inflorescence often fail to open at all. Each flower may potentially produce one capsule which contains a maximum of 2 seeds, although in many cases only one seed per capsule is produced, and, on average, about 1.3-1.6 seeds are produced per capsule. Table 4.12 below shows the number of buds, flowers and fruits produced on average per flowering plant, and the average number of seeds produced per developed capsule. Overall, 16.5% of plants produced an inflorescence annually (see Table 4.13).

Table 4.12

Annual flower, fruit and seed production. Means per flowering plant, seeds per ripe capsule.

Year	Site	Buds	Flowers	Fruits	Seeds
1973	Widdybank	17.4	13.1	9.0	1.55
	Cronkley	NR	NR	NR	NR
1974	Widdybank	12.0	7.0	6.9	1.50
	Cronkley	12.3	9.1	7.3	1.39
1975	Widdybank	12.2	7.3	4.9	1.33
	Cronkley	NR	NR	NR	1.29

Table 4.13 shows the annual percentage of plants that produce flowers in each site. The average percentage of plants producing an inflorescence in a year are 16.5%, but there is considerable variation between sites and years, from about 7% in several records to nearly 50% in 7:2 in 1975. Analysis of variance, using transformed data, and bearing in mind the provisos of section 3.5.2 indicates that there are very significant differences between years and between sites, with no evidence of interaction between sites and years (using Widdybank data only). Between sites, 6:1 is significantly lower than average ($P \ll 0.001$) and 7:2 is significantly higher than average ($P \ll 0.001$). Between years, 1974 is significantly lower than average ($P \ll 0.001$) and 1969 and 1975 are significantly higher than average ($P \ll 0.001$). The figures for Cronkley (Black Ark) given separately parallel this pattern, except for 1975, where there was no recorded flowering.

4.7 Life cycle and reproductive strategy.

4.7.1 Species biology summary.

Polygala amarella is a short-lived evergreen perennial reproducing entirely by seed. It may enter the reproductive phase in its second year, but most individuals flower first when they are 3 or 4 years old, and they may continue to flower continuously or intermittently for up to 4 further years. The average life expectancy of a Polygala plant at birth is about 4.5 years, but many plants can live much longer than this, and the estimated average total turnover time, based on the original mixed-age populations, is 8-9 years, (although in one site it may be as high as 35 years). The annual mortality rate of all plants, excluding seedlings, calculated over the period 1969-1975 has been 0.241, with a much higher rate of disappearance over the winter period than the summer.

Polygala amarella

Table 4.13

Percentage of plants in each sample producing flowers

Year	Site					
	6:1	7:1	7:2	D.S.	Total Widdybank	Black Ark Cronkley
1969	20.0	34.5	32.5	16.7	28.2	14.1
1970	16.1	18.7	18.9	7.3	15.4	8.9
1971	13.3	10.9	23.4	14.7	16.0	12.7
1972	9.6	11.8	29.3	20.0	14.8	20.5
1973	7.8	7.9	30.9	12.5	15.1	5.7
1974	7.4	17.8	12.5	8.0	10.5	4.5
1975	9.5	21.4	48.3	27.3	21.1	0.0
Averages	11.0	16.3	26.0	13.3	16.5	9.4

On average, 16.5% of plants flower in any one year (although there are considerable variations between years), and these numbers consist of a variety of ages of plants, with some plants flowering for the first time, others for the second, third or fourth time. A flowering individual produces a branched or unbranched inflorescence, which continues to expand through the summer and which may produce up to 30 (or, very exceptionally 50 in the case of a vigorous branched inflorescence) flower buds. A number of these, particularly the ones which develop later, clustered around the apex, fail to open and cannot produce seed. Those flowers that do open may produce a capsule which contains up to 2 seeds, although frequently there is only one. Knuth (1906-9) after Müller states that Polygala amarella may be insect-pollinated or self-pollinated, cross or selfed, although Fearn (1971) and Elkington (1978) indicate that it is inbreeding, and predominantly self-pollinated, in Teesdale. No doubt the continental populations studied by Müller lived under different conditions and inbreeding appears to be the rule in Teesdale.

The seeds themselves are relatively heavy, (ave. 0.86mg*, Marren unpublished data) and about 1mm x 2mm in dimensions. Dispersal of seed is apparently very restricted (Doody 1975) although the seeds possess two elaiosomes (oil bodies) which may assist dispersal, as described by Ridley (1930) for P. vulgaris: "This oily substance is very attractive to ants, and they seek for fruits and seeds so furnished, and carry them to the nest, very frequently eating off the oil body on the way and then dropping the seed". Sheep often graze inflorescences with ripe seed, and this may be voided in a viable state, in the manner shown by a

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* Average of 122 seeds from three years.

number of other species (e.g. Hansen, 1911; Ridley, 1930). A search was made for viable seed in collected sheep droppings but none was detected, as one might expect for the seeds of a species with such limited distribution and fecundity. However this method, coupled with occasional longer distance accidental dispersal by mammals (and especially man) may allow new colonies to establish infrequently. The number of germinated seedlings recorded has varied considerably, around an average of 28 per 100 plants per year, from 222 per 100 in 1969 to 11 per 100 in 1974.

4.7.2 Life cycle.

Using all the average data collected over the 6 years, it is possible to construct a stylised life cycle diagram for the behaviour of the species on Widdybank Fell. Although it is not representative of any particular year, and a number of assumptions are made in its construction, it gives a useful indication of those points of the life cycle where loss of individuals or potential individuals occurs.

The diagram (Fig. 4.5) is based on the following figures and assumptions:

1. An annual average mortality of 25% (in fact 24.1%) for adult plants as calculated from Table 4.5.
2. An annual average flowering percentage of 16% (actually 16.5%; see Table 4.13) i.e. 16 plants amongst every 100 produce an inflorescence, or start to produce one.
3. Figures for a 35% loss between buds and flowers, 24% loss between flowers and fruits, 27% loss between ovules and seeds, and a 35% loss of inflorescences before seed is shed are considered, but are not part of the calculation since the number of seeds produced was counted directly, and therefore reflects these losses.

4. An annual average production of 145 seeds per 100 plants.
5. An annual average recruitment of seedlings of 17 per 100 plants. This differs from the figure quoted above (28 plants per 100) because the period 1970-1976 has been considered, in order that this may be directly compared with seed produced over the period 1969-1975. Seedlings recorded in 1969 were vital for the species survival, but they have not been included in this analysis since the amount of seed from which they arose is unknown, and they give the impression of a better ratio of seedlings germinated : seeds produced than is really the case.
6. Emigration is assumed to be equal to immigration, although this may not be the case.
7. Seed viability is known to be ± 100% (Doody, 1975) under optimum conditions, and assumed to be similar on the Fell.
8. Flowering is assumed not to affect the mortality of plants.
9. Overwinter loss of seedlings is calculated as a 25% loss over a 6 and 9 month period.

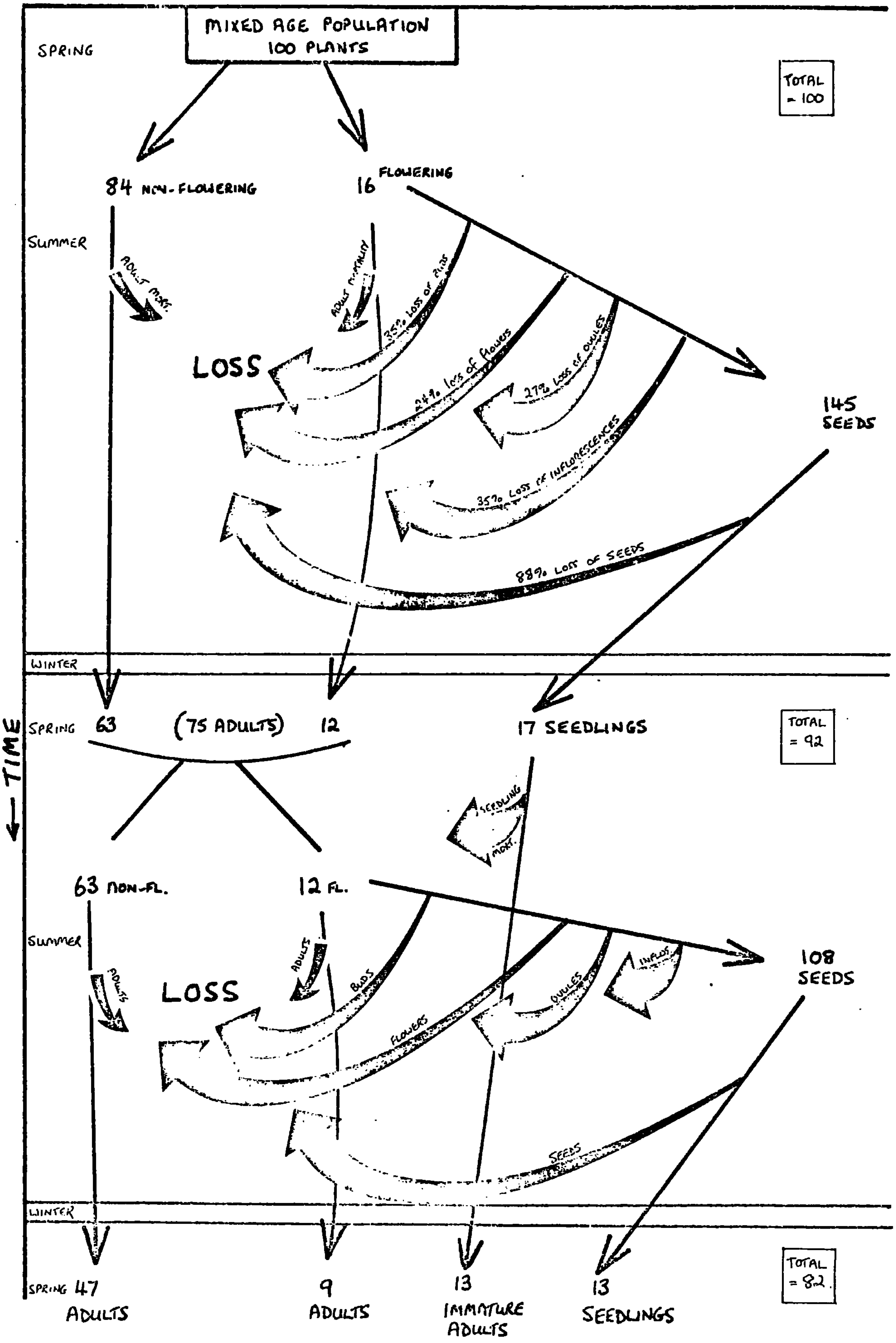
Two factors stand out. Firstly that the population is declining at this observed average performance. As described, the exceptionally favourable seedling year in 1969 has been excluded, and it is immediately clear that such years are vital to the species' survival in Teesdale. Secondly, the greatest single loss of potential individuals occurs between seed production and seedling germination: 88% of seeds are lost, despite their reasonably large size.

4.7.3 Factors operating at each stage to reduce the intrinsic rate of increase of the population.

a. <u>Mortality of established plants.</u> This acts at a more or less constant rate, irrespective of the age of the plant. There may be variation between years, although only one

FIG. 4.5 POLYGALA AMARELLA

LIFE-CYCLE DIAGRAM.



year 1969-1970 was found to be significantly different ($P < 0.001$) to the others. Since mortality is more or less independent of age for all plants including seedlings, it may be presumed that such a difference is due to some widely operating external factor, such as climate, or alteration of grazing level that has affected all plots similarly. Site comparisons, however, indicate that there is no intrinsic rate of mortality for the species under Teesdale conditions. Between most plots, there was no significant difference in mortality rates, but 6:1 had highly significantly lower mortality ($P \ll 0.001$) than all other plots (sect. 4.7.4). Moreover, plants in this plot had a greater life expectancy than those of other plots (Table 4.4), a much higher mixed-age population half-life, and a higher half-life for most additions up to Summer 1971 (Table 4.3). Plants in 6:1 had an estimated turnover period, based on the half-life of the mixed age population of almost 35 years, compared to 8.3 years for the Widdybank average, or 6 years for the "poorest" site. Site 6:1 had one of the larger populations, so there are no grounds for supposing that this very marked difference is spurious. Accepting that plants in 6:1 are genuinely long-lived, then it is necessary to accept that small-scale factors operating within a given climate, and within a reasonably homogeneous vegetation (in general appearance) can have a very considerable effect on the length of life of individuals of this species, and that this difference is consistent. This is discussed further with reference to site differences (Sect. 4.7.4) but it is relevant to consider here the likely causes of mortality of adult plants. These include: removal by herbivores; drought, either actual or "physiological"; competition, for space, nutrients, light etc.; below-ground predation; slug, fungal, or other comparable damage sufficient to cause death, perhaps in combination with other factors; rotting of rosette or rootstock; instability of substrate causing partial or complete uprooting; inherent mortality. It is of interest that mortality is significantly higher ($P < 0.001$; see Table 4.7) in winter per unit time than in summer. Grazing, flowering and fruiting, and probably growth are all more or less confined to the summer 6 months, suggesting that other factors are more important in determining the total mortality. If, however, the spring record was taken some time after the first growth had been made, early growing season mortality (often found to be a major mortality period) would be included in the winter figures, although it is unlikely that this could account for all the seasonal mortality differences, and the first spring record was normally intended to be at the start of the growing season. It would certainly seem probable, generalising from other plants _a priori_, that considerable mortality might take place as growth started in early spring, but was halted by the severe spring frosts that regularly occur.

The majority of these factors, particularly as the major factors are unknown, are difficult to control in a natural situation, and - for conservation purposes - it is best to accept the high turnover rate until more information is available.

b. _Abortion of buds._ A high number of potential seeds are lost in this way, although the high subsequent losses of fruits, ovules, whole inflorescences, and seeds in the soil render the loss less significant. The loss is difficult to control, although it is probable that increased growth under protection from grazing would allow more buds to develop to fruit.

c. Loss of flowers. 24% of flowers do not develop into fruit, excluding those lost when whole inflorescences are lost. This may not be an accurate reflection of the normal situation, as the sample available was small. Presumably the losses result from inadequate pollination, desiccation, predation, damage, and inherent factors. These are not easily controlled.

d. Loss of ovules. Each capsule may develop a maximum of 2 seeds, although in many cases they do not. 27% of ovules do not develop into seeds, in this way. Presumably poor pollination is the cause, or inherent infertility, although it would be useful to have data for populations in different situations, or the present population in the absence of grazing at flowering time.

e. Loss of whole inflorescences. 35% of inflorescences (using data from two years only) may disappear, and their loss is presumed to be due to grazing by sheep or rabbits. Their loss represents a very considerable loss of potential new plants, despite the disappearance of seeds in the soil subsequently, and the remedy is clear, providing other factors can be kept reasonably stable, i.e. grazing should be prevented, on a trial basis, over very limited areas containing flowering *Polygala* plants for as short a time as necessary. The results should be closely monitored, preferably on the lines set out in this study, with adjustments made if necessary.

f. Loss of viable dispersed seed. *Polygala* seed apparently distributes itself over a very short distance, and making a number of reasonable assumptions, as described, it appears that 88%, on average, of seeds never come above ground as seedlings. This is, clearly, a highly critical phase of the life-cycle yet it is the one about which the least is known. The possible causes of this loss are manifold, and include: predation by invertebrates* or small mammals; desiccation; loss of viability; below ground (or otherwise unseen) germination and subsequent mortality; excess of emigration over immigration e.g. if there was an ants' nest nearby such that seeds tended to be moved out of the quadrat towards this; irreversible (within the period of viability of the seed) burial; disease and rotting.

No estimates can be made about the relative importance of these possible factors, nor whether a particular one, or any others, operates at all. Much of this mortality could, no doubt, be overcome by manipulation - i.e. collection of the seed, storage in ideal conditions over winter, followed by distribution at the optimum time in spring - early summer. There is no evidence of a freezing requirement (Doody, 1975), and indeed freezing appears to delay germination (Doody, unpublished data). This particular suggestion is made only because it is clear that the Teesdale population of _Polygala amarella_ is seriously endangered.

2. Seedling mortality. Seedling mortality occurs at a rate similar to that of adult plants. Similar factors operate to cause mortality, although grazing by large herbivores is unlikely to be a factor, whereas damage by slugs, snails or other ground-living invertebrates**is likely to be of particular importance.

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* Coulson and Whittaker (1977) and Coulson (1978) give figures for the soil fauna dry weights and numbers per M^{-2} in Teesdale limestone grassland. Nematodes and Craneflies, for instance, are exceedingly abundant, with well over 1 million nematodes per M^{-2} of grassland.

** Coulson and Whittaker (1977) record the presence of 16 species of snails and slugs in Upper Teesdale.

h. <u>Percentage flowering.</u> Only 16% of the plants in the population produce flowers, although 86% is of an age capable of doing so (see Fig. 4.4). It has been shown that site factors and annual factors both affect the percentage of plants that flower, in some way, and it is likely, therefore, that other more controllable factors may also influence this percentage, e.g. grazing may tend to reduce this percentage by reducing the vigour of plants and their ability to recover after flowering, and possibly by gradually selectively removing the more floriferous plants.

4.7.4 Site differences and their significance.

It has been mentioned several times that consistent differences exist between plants in separate sites, and that, in some cases, these have been shown to be highly significant. The observed differences, in summary, are as follows:-

1. 6:1 has a lower mortality ($P < 0.001$), higher half-life for its mixed-age population and subsequent age cohorts, and greater life expectancy for individuals than all other sites.
2. 6:1 has the lowest annual flowering percentage ($P \ll 0.001$), and 7:2 has the highest ($P \ll 0.001$).
3. 6:1 has the lowest annual average recruitment of seedlings, although the difference was not shown to be significant.

The general significance of observed site differences is discussed in Chapter 9. It is discussed here only with respect to the dynamics of <u>Polygala amarella</u>. 6:1 is clearly very different in some way from the other <u>Polygala</u> sites, yet it is difficult to be sure why. 6:1 lies in reasonably stable, closely-grazed turf, (see sect. 4.2) away from any eroding sugar limestone edges, on a gentle west-facing slope. The remaining three Widdybank sites have similar aspects generally; Draba stone is very atypical in that the site lay over a boulder on which the Polygala was growing in a moss/lichen substrate. Part of the site consisted of bare rock, and part of dense Calluna. Quadrat 7:1 was apparently similar to 6:1, with a closed turf of Sesleria and Festuca ovina, although it was probably damper as indicated by the presence of Plantago maritima. Quadrat 7:2 was also apparently similar to 6:1 and there was no particular evidence that it was damper. Both quadrats at 7, and 6:1 are grazed heavily. Thus, no obvious environmental differences suggest themselves as possible causes of the lower mortality and lower flowering and recruitment at 6. The three factors are to some extent interdependent, and the possible reasons can simply be guessed at as differences in drainage, or other hidden environmental factors, competition from surrounding vegetation, or some combination of these, or recent historical factors (see Chapter 9).

4.7.5 Reproductive strategy.

The main features of populations and individuals of Polygala in Teesdale have been described. In summary, the species reproduces entirely by seed. Plants normally enter the reproductive phase at 2-4 years old, and may then continue to reproduce for some years. After flowering, a relatively small number of quite large seeds are produced which can give rise to seedlings with as high a likelihood of survival as adult plants. The average rate of loss of individuals from the population is about 25% per annum. The general strategy is thus a cautious one, with a small proportion of the individuals producing quite a small number of large seeds, and the intrinsic rate of increase is not high in comparison to many plants, (e.g. Salisbury 1942). Polygala is generally a plant of closed or reasonably closed vegetation.

Since it has no method of vegetative reproduction, it is essential that seedlings establish as fast as plants are lost. Seedlings are, clearly, able to establish themselves in closed turf, and, although the loss of seed is high, the survival of seedlings is good. The ability of plants to persist in the turf for a number of years, and to flower repeatedly are of evident importance to the species, although the loss rate is much higher than for many seed-reproducing perennials (cf. Viola rupestris, and the work of Tamm, 1956,1972), and the population suffers accordingly.

In Teesdale, Polygala amarella is considered to be a habitual inbreeder, (Fearn, 1971), and thus its innate variability is likely to be low. Its presumed survival from before the Forest maximum in apparent relative isolation (Elkington, 1978) suggests a degree of ability to cope with changing conditions, but we cannot be certain that it was not an outbreeder at some stage previously (cf. Knuth, 1906-9), and we may be looking at the remnants of a once more varied population that have now less flexibility to survive changing conditions.

It is not possible to generalise from observations on the Teesdale plants to those of other areas in Britain. A population in Wharfedale, observed briefly in 1974, showed a number of obviously different characteristics. The plants were vigorous branched structures, and their size, and diameter of the woody rootstock suggested a considerable age. Very large numbers of flowers were produced (224/rootstock*) by an apparently high proportion of the population (c. 70%, in a small sample), and large numbers of seed were beginning to set. The situation was

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* from a sample of 23 plants, May 1974.

at a much lower altitude, further south, and with limited grazing pressure from cattle only, and the plants have had quite a different history. The evidence therefore suggests that their life strategy, and their success are different to the populations studied in Teesdale.

Chapter Five

Gentiana verna

5.1 Introduction.

Gentiana verna is a native of Britain, confined to two widely separated areas, one in Western Ireland and one in Upper Teesdale and adjacent areas. Within each of these relatively large areas, the plant is locally abundant, although it is a protected plant under the "Conservation of Wild Creatures and Wild Plants Act, 1975" and is listed as an endangered species by Perring and Farrell, 1977.

It is a small, perennial evergreen herb, with a fibrous root system, and the capacity for producing short underground stolons which emerge to end in a tuft of leaves. Elkington (1963) records that these stolons may be from 2-15cms long, branched or simple, although observations on plants in cultivation in Durham have shown that stolons of at least 25cms may occur. The rosettes thus produced become indistinguishable from those produced from seed, and they may themselves produce stolons when established. In this study, all rosettes that were not demonstrably attached to another were regarded as individuals, the units of the population, and it would appear that the vast majority of the plants in the populations under study were produced by this method of vegetative reproduction.

Anderson (1961) described Gentiana verna as "Delightful, but often short-lived" in gardens, and both Elkington (1963) and Bartlett (1975) record that wild-collected plants have survived for up to 4 years in cultivation. It is thus generally recognised as a short-lived plant, often, though by no means always, dying after flowering, although plants appear to be capable of persisting in the vegetative state for at least 7 years. It is apparently completely frost-hardy.

In Teesdale, this species is largely restricted to open grassland, and is intolerant of shading or intense competition. It occurs almost entirely on grassland overlying "sugar limestone" or unaltered limestones, generally on the slightly damper sites, but it may also occur in grassy patches amongst heather (*Calluna vulgaris*), Crowberry (*Empetrum nigrum*) or other dwarf shrubs.

5.2 Study sites.

Six separate permanent quadrats with associated sample plots were established, five on Widdybank Fell, and one on Cronkley Fell.

Quadrat 1:1 lay in heavily sheep-grazed closed turf just above a markedly flushed area. The dominant grass was *Festuca ovina*, with smaller amounts of *Koeleria gracilis*, *Briza media*, *Carex panicea* and *C. flacca*, *Galium sterneri*, *Selaginella selaginoides*, *Prunella vulgaris*, *Linum catharcticum* and *Campanula rotundifolia*. Doody (1975) shows a map of the vegetation in one metre of this quadrat in 1970. The quadrat is two metres long, and there was little observable change during the period of study, except that one corner and edge progressively eroded into the adjacent hollow.

Quadrat 4:1 was 3 metres long. It had a vegetation cover of closed, heavily-grazed turf consisting largely of *Sesleria caerulea* and *Festuca ovina*, with a large clump of *Calluna vulgaris* and more scattered plants of *Kobresia simpliciuscula*, *Carex flacca*, *Campanula rotundifolia*, *Potentilla erecta*, *Thymus drucei*, *Antennaria dioica*, *Polygonum viviparum* and *Selaginella selaginoides*. The plot lay near the top of a knoll, a few metres above an extensive spring-head area. A limestone boulder abutted on to the quadrat, and this may be a significant factor in increasing the water supply to part of the quadrat, by increased runoff, in the manner observed by Savile, 1972.

Quadrat 7:2, which was also recorded for *Polygala amarella*, was closely-grazed and dominated by *Festuca ovina* and *Sesleria caerulea*, with smaller amounts of *Helianthemum chamaecistus*, *Hieracium pilosella*, *Lotus corniculatus*, and significant amounts of the mosses *Dicranum scoparium* and *Rhacomitriun lanuginosum*. The quadrat lay on thin sugar limestone soil, and was apparently drier than other gentian quadrats.

Quadrat 8:3, 2 metres long, contained considerable quantities of *Calluna vulgaris* in a turf of *Kobresia simpliciuscula* and *Carex flacca*, with lesser amounts of *Potentilla erecta*, *Polygala serpyllifolia* and *Selaginella selaginoides*. A major sheep track passed very close to the quadrat.

Quadrat 8B:4 was situated in a hummocky area adjacent to a large area of *Calluna vulgaris*. Both *Calluna vulgaris* and *Empetrum nigrum* were present in the quadrat, and the grazing pressure was generally rather low, allowing a much taller turf development. The dominant grasses in the turf were *Sesleria caerulea* and *Festuca ovina* with smaller amounts of *Koeleria gracilis*, *Briza media* and *Kobresia simpliciuscula*. Associated species were *Campanula rotundifolia*, *Thymus drucei*, *Viola lutea* and *Polygonum viviparum*.

Quadrat 10:1 on Cronkley Fell was situated inside a large exclosure. Sheep were excluded, and although Doody (1975) recorded that there was very little rabbit-grazing over the period 1969-1972, this increased considerably in subsequent years, and the hummock in the quadrat was used as a "latrine" for at least 2 years. The turf was dominated by *Sesleria caerulea* and *Festuca ovina*, and was very well-grazed, although not by sheep.

5.3 Population flux.

Seven years of recording have revealed no very clear-cut trends in the Gentiana populations on Widdybank or Cronkley Fells except that the overall numbers of rosettes appears to be essentially stable

On Widdybank Fell (See Fig. 5.1 and 5.2) there are shown to be constant fluctuations and a general increase in the total numbers of rosettes in all quadrats, with the final Autumn 1975 record 46 plants (14%) higher than the Spring 1970 record. A peak of plant numbers was reached in early 1971 (corresponding to a peak in several individual quadrats), and the initial Spring 1970 total of 330 plants was the lowest recorded. The fluctuations are a facet of the relatively short life of individual plants (mean 3.2 yrs), and the mechanics of these changes are shown in Table 5.1. It is noticeable that the fluctuations do not have a particular seasonal pattern, although the spring figure is often the lowest of the three records within a year. This reflects the observation that production of new rosettes is significantly lower per month in the winter period ($P<0.001$) while mortality remains more or less constant throughout the year.

The rapid increase through 1970 to Summer 1971 can be seen to be caused largely by a much higher than average number of additions, with about average mortality. Individual sites show a generally similar pattern to the total figures, with frequent fluctuations. All sites except 7:2 had more plants in at the end of recording than at the start. No site made especially marked gains, although 4:2 showed a 75% increase over one 2-year period, much of which has subsequently been lost.

5.4 Mortality rates and Life expectancies.

5.4.1 As indicated briefly under Population flux, rosettes of Gentiana verna have a relatively short life, estimated at 3.2 years, on average, with a mean annual loss rate of 20-30% of all plants

FIG.5.1 GENTIANA VERNA. POPULATION FLUX IN FOUR QUADRATS, 1968-1975.

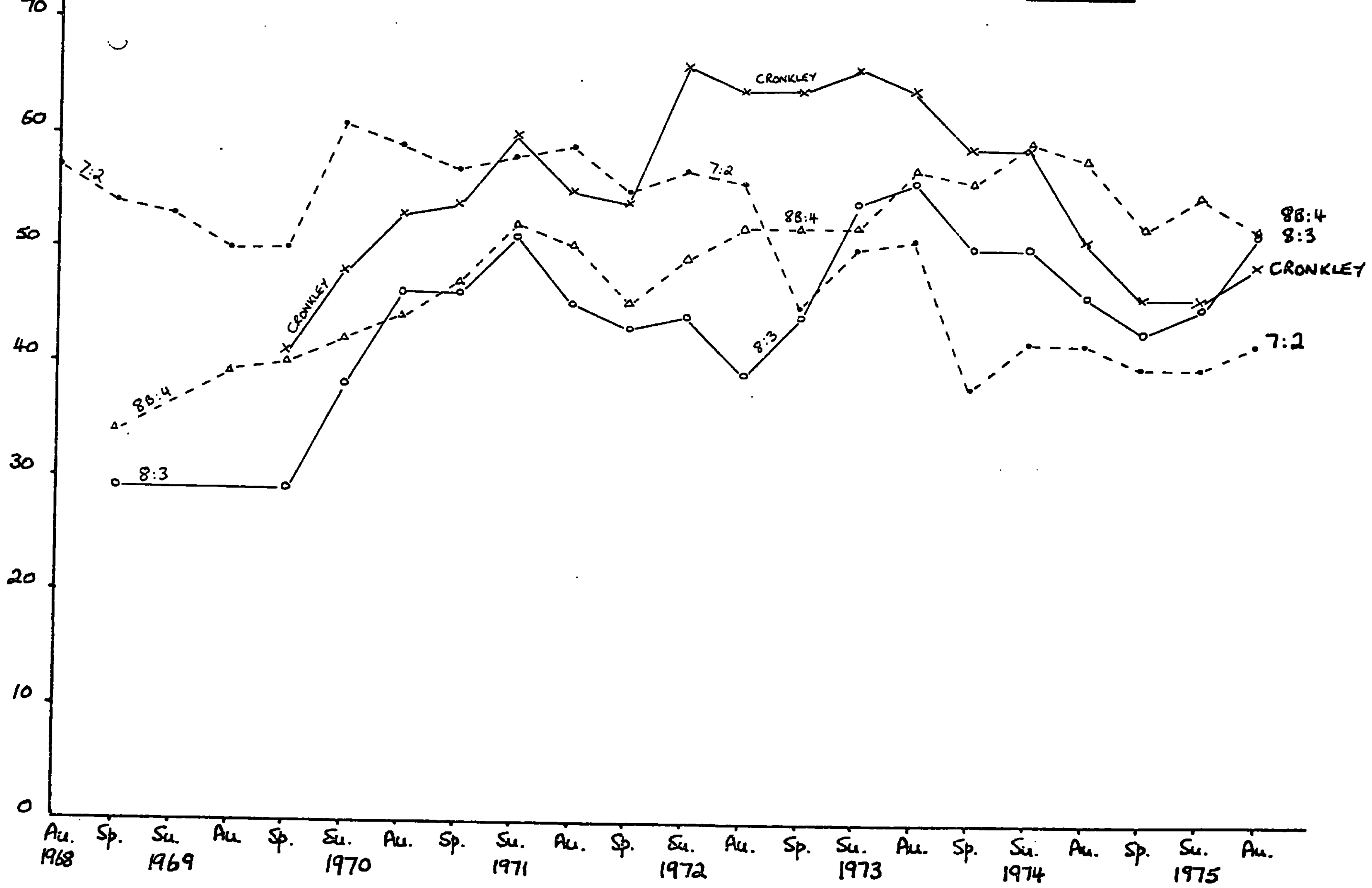

FIG. 5.2. GENTIANA VERNA.

POPULATION FLUX IN TWO QUADRATS, 1968-1975.

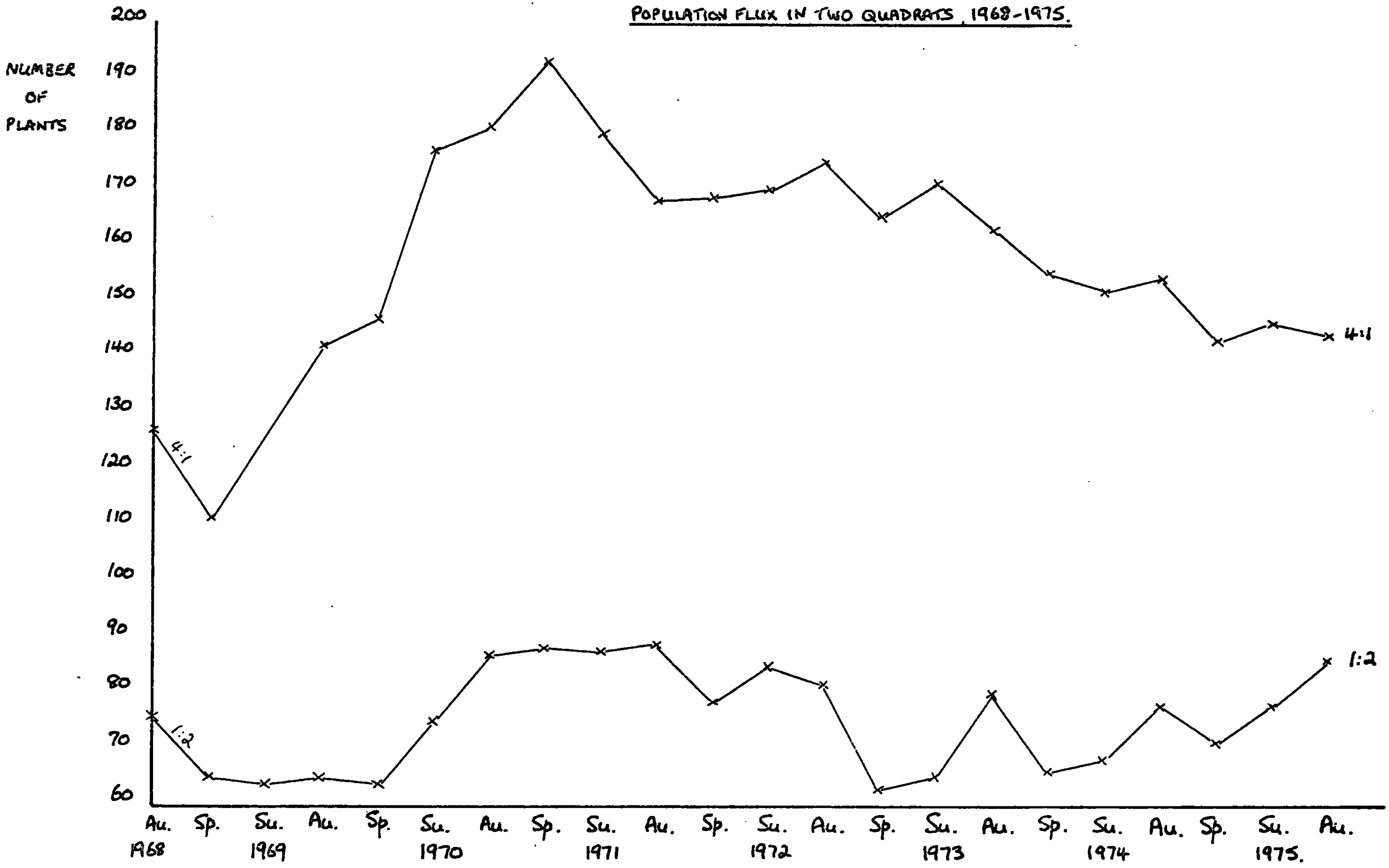

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Table 5.1

Separate additions (new rosettes) and mortalities
in Widdybank Fell permanent plots

Season	Additions in each season	Mortalities in each season	Change in pop. numbers + or −	Total pop. numbers
Autumn) 1969	(96)*			
Spring)	79	77	+2	330
Summer) 1970	91	28	+63	393
Autumn)	54	30	+24	417
Spring)	75	61	+14	431
Summer) 1971	40	43	-3	428
Autumn)	25	42	-17	411
Spring)	30	50	-20	391
Summer) 1972	50	36	+14	405
Autumn)	26	27	-1	404
Spring)	12	47	-35	369
Summer) 1973	29	6	+23	392
Autumn)	50	35	+15	407
Spring)	18	60	-42	365
Summer) 1974	47	44	+3	368
Autumn)	25	18	+7	375
Spring)	34	63	-29	349
Summer) 1975	31	16	+15	364
Autumn)	43	31	+12	376

( )* includes an estimated figure

(Table 5.5), although considerable variation exists between sites and years.

5.4.2 Age specific mortality.

Graphs showing the decline of plants in individual year cohorts plotted on a log scale against time (Doody, 1975) indicate that the mortality of plants may be exponential, and a function only of numbers of plants and not of their age. Figures for age cohorts from all years were therefore pooled and compared over their life span for mortality rates in each age-class (Table 5.2) using data from all Widdybank Fell sites.

As explained in Section 3.5.3., the study has not continued long enough to allow the comparison of equivalent numbers in each age class. There are decreasing numbers of plants being considered in each age class, and there is thus an increase in the variance of estimates as the sample size becomes smaller. Preliminary inspection of the data indicates that mortality is highest among 1-3 year-olds, particularly from 1-2 years, but a χ^2 test on all the figures indicates that there are no significant differences between the survival of age-classes, even at the 5% level. The variation in mortality rates amongst different years precludes any clear distinctions from being made. It must be assumed, therefore, that mortality in Gentiana rosettes is independent of age, although there are indications that mortality may be higher among 1 to 3 year old plants, and more or less constant amongst all other age classes.

On the assumption that mortality is independent of age, it is reasonable to calculate half-lives for the populations in each quadrat, as an indication of the length of life of plants, and the rate of turnover of populations. Table 5.3 shows the half-lives of the mixed-age populations and subsequent additions up to 1971 in each site, calculated on the basis of the number remaining

Gentiana verna

Table 5.2

Year class survival : Age classes compared.

Year First Rec.	Period of survival in years .							
	0	1	2	3	4	5	6	7
1968 Mixed-age	Incomplete	Incomplete	138	91	66	51	36	27
1969 adds.	104	71	51	34	27	20	17	
1970 adds.	208	151	107	86	68	50		
1971 adds.	118	96	73	52	38			
1972 adds.	101	81	54	39				
1973 adds.	89	57	34					
1974 adds.	88	63						
1975 adds.	106							
Totals in ea. year class	814	519	319	302	199	121	53	27
Prop. surviving		0.733	0.700	0.714	0.757	0.752	0.746	0.750
Mort.		0.267	0.300	0.286	0.243	0.248	0.254	0.250
Significance		NS	NS	NS	NS	NS	NS	NS

Gentiana verna

Table 5.3

Half lives of mixed age populations
and age-cohorts (in years).

Cohort	Sites						
	1:2	4:2	7:2	8:3	8B:4	Cronkley	All Sites
Mixed age pop.	1.78	2.24	1.44	1.16	2.57	2.48	2.35
Aut. 1969 adds.	1.09	3.30	1.82	NR	2.17	NR	
Spr. 1970 adds.	1.93	2.58	6.30	2.39	2.57	NR	
Sum. 1970 adds.	2.39	2.17	3.01	1.93	5.33	2.48	2.48
Aut. 1970 adds.	1.93	2.04	0.39	3.15	3.85	1.93	2.17
Spr. 1971 adds.	1.65	2.39	2.24	4.62	1.41	1.09	2.10
Sum. 1971 adds.	1.24	2.39	4.33	4.95	3.47	3.01	2.89

Calculated to Autumn 1975, except where cohort had died out previously.

at Autumn 1975. In Site 8:3, none of the original population was left at Autumn 1975, and the half life was therefore calculated up to the last record of any plants remaining. On the basis that half life is roughly ¼ of the total turnover time, we can estimate total turnover times as follows, based on the original mixed-age population half-lives:-

Table 5.4

Estimated total turnover time of plants in each site.

Site	Turnover time, years, approx.
1:2	7
4:2	9
7:2	6
8:3	4½
8B:4	10
Cronkley	10
Overall	9

The differences are by no means as marked as in Polygala, but there are indications that plants live longer in site 8B:4 and possibly Cronkley, although the variation amongst individual year-classes is great.

5.4.3 Life expectancy values.

Life expectancy values (Le) have been calculated for plants in each site, as explained in 3.5.3., based on the recorded length of life or projected length of life of all individuals added since recording began. The figures for plants in each site are presented in Table 5.4b below.

Table 5.4b

Life expectancies for individuals in each site based on the period 1969-1975.

Site	Le (years)
1:2	3.18
4:2	4.85
7:2	3.62
8:3	5.07
8B:4	5.65
Cronkley *	4.11
Average	4.34

* Calculated over the period 1970-1975 only.

These figures give a slightly different indication of which plots have the longest-lived plants (the technical reasons for the difference between Le and ½-life estimates are discussed in 3.5.3), although plants in 8B:4 again appear to have the longest life-span. The average length of life of all plants over all quadrats, using the formula:

$$L_{\bar{x}} = \frac{2-M}{2M} \quad \text{where } M \text{ is the annual mortality}$$

is 3.16 years (see Table 5.5).

5.4.4 Annual mortality rates.

Table 5.5 compares the annual mortality of all plants in Widdybank sites, using Autumn records only. The figures represent the number at risk in each autumn and the number surviving at the subsequent autumn, and the proportions surviving each year overall are calculated. Thus the mortality of new rosettes between appearance and their first autumn is not included.

The average annual mortality over all years was 0.273 (i.e. an average of 27% of plants die each year), and analysis of the table as explained in section 3.5.4 suggests that there are no differences

Gentiana verna

Table 5.5

Year class survival - Years compared.
All Widdybank plots, Autumn figures.

Year Class	Period of survival							
	1968	1969	1970	1971	1972	1973	1974	1975
1968 orig. pop.	Incomplete records	Incomplete records	138	91	66	51	36	27
1969 adds.		104	71	51	34	27	20	17
1970 adds.			208	151	107	86	68	50
1971 adds.				118	96	73	52	38
1972 adds.					101	81	54	39
1973 adds.						89	57	34
1974 adds.							88	63
1975 adds.								106
Totals	-	104	417	411	404	407	375	374
Prop. Surviving.			0.683	0.703	0.737	0.787	0.705	0.715
Annual Mort.			0.317	0.297	0.263	0.213	0.295	0.285
Significance			NS	NS	NS	NS	NS	NS

Mean proportion surviving = $\frac{1540}{2118}$ = 0.727

Mean mortality = 0.273

Ave. length of life $\frac{(2-M)}{(2M\ )} = \frac{1.727}{0.546} = \underline{3.16 \text{ years}}$

Gentiana verna

Table 5.6

Annual mortality

	Sites						Annual Averages
	1:2	4:2	7:2	8:3	8B:4	Cronkley	
Autumn 1968 - Autumn 1969	0.46	0.26	0.49	NR	NR	NR	(0.37)
Autumn 1969 - Autumn 1970	0.66	0.25	0.46	NR	0.38	NR	(0.39)
Autumn 1970 - Autumn 1971	0.40	0.33	0.25	0.52	0.27	0.25	0.34
Autumn 1971 - Autumn 1972	0.29	0.22	0.39	0.31	0.24	0.25	0.27
Autumn 1972 - Autumn 1973	0.34	0.28	0.27	0.03	0.10	0.22	0.24
Autumn 1973 - Autumn 1974	0.35	0.29	0.33	0.36	0.18	0.31	0.30
Autumn 1974 - Autumn 1975	0.26	0.31	0.26	0.20	0.38	0.31	0.29
Site Averages	0.39	0.28	0.35	0.29	0.25	0.27	0.29

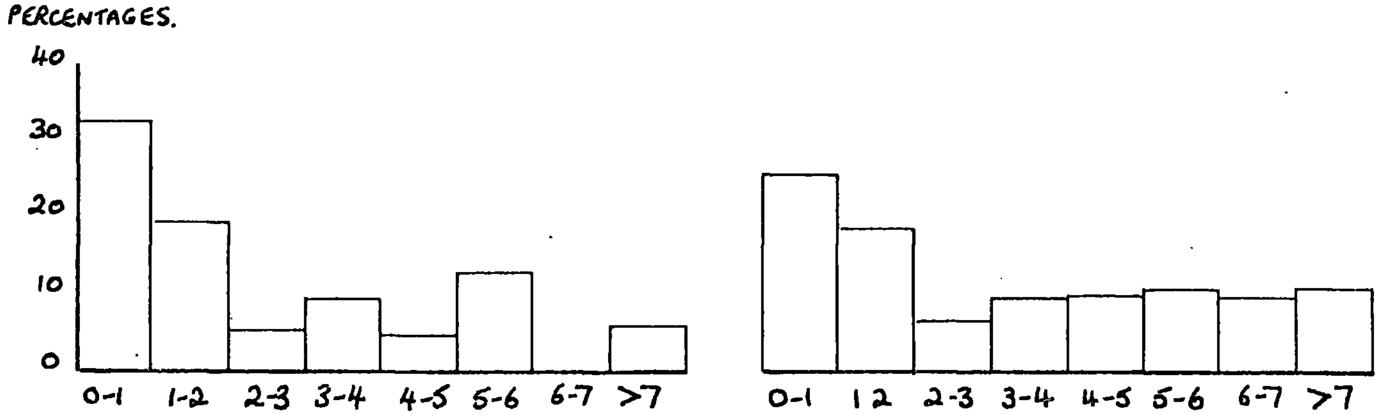
in mortality between years. However, this method of mortality analysis does not take into account site differences, assuming that they all behave in a similar fashion. Table 5.6 shows the separate annual mortality figures for each site, and these are analysed by the considerably more sensitive method explained in 3.5.4. For the purposes of analysis, sites 8:3 and Cronkley were excluded so that all years could be considered, and a figure for 8B:4 Autumn 1968-Autumn 1969 was calculated using the standard "missing-plot" technique (Bailey, 1969). This analysis indicated that significant differences existed between sites ($P \ll 0.001$), and between years ($P < 0.01$), and that there was a high degree of interaction between years and sites. Partition of the data indicated that differences in 1968-1969 and, in particular 1969-1970, were the main contributions to the differences between years, and that these differences were significantly different to the mean ($P < 0.02$). It was found that the main sources of between-site variation were 8B:4 and 1:2, and that 8B:4 had a significantly lower mortality than average ($P < 0.001$) while 1:2 had a significantly higher mortality than average ($P < 0.001$). The exact source of site-year interaction could not be clearly defined, although presumably this degree of residual variation accounts for the failure of analysis of Table 5.5 to detect a significant difference in mortality in the period 1969-1970. When 1968-1970 mortality was removed from the data, there was found to be no significant difference between the other years.

5.4.5 Age structure of the population.

Attempts were made to age individual rosettes of Gentiana verna in the field, but no certain repeatable method was found. Therefore, the only way in which the age structure of the population can be determined is by regular recording until the age of all plants in

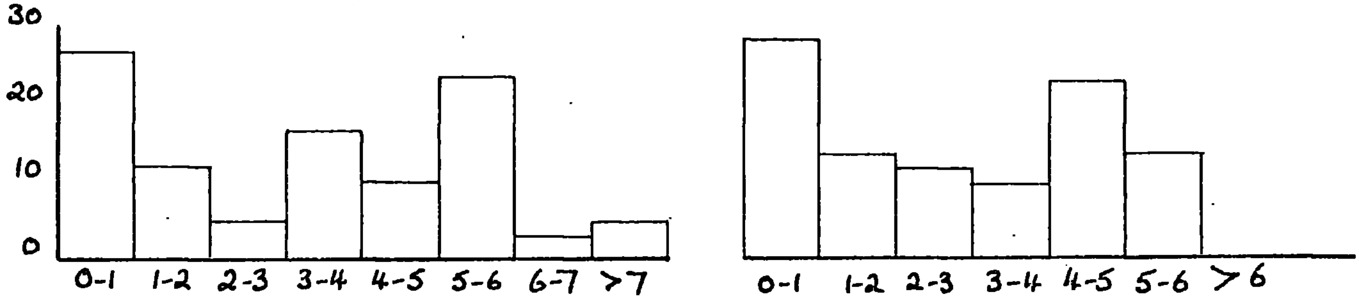
FIG. 5.3 GENTIANA VERNA.

AGE-CLASS DISTRIBUTIONS.



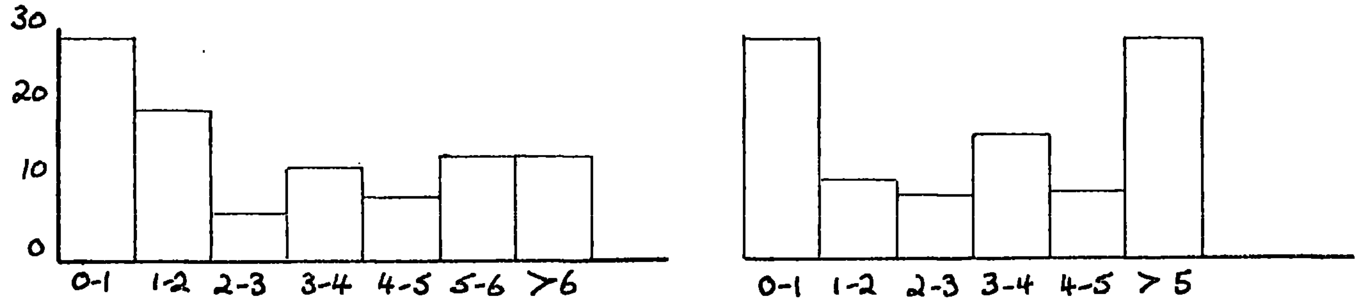
1:2 (86 PLANTS)

4:1 (144 PLANTS)



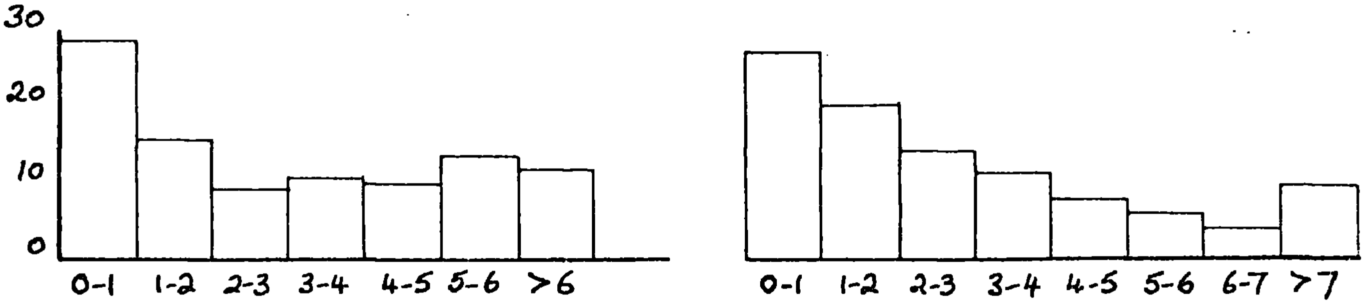
7:2 (42 PLANTS)

8:3 (52 PLANTS).



86:4 (52 PLANTS)

CRONKLEY (49 PLANTS)



WIDDYBANK FELL AVERAGES.

"MODEL" POPULATION
27% ANNUAL MORTALITY.

Gentiana verna

Table 5.6b

Age class distribution of populations in permanent plots at Autumn 1975. Percentage figures.

Site	Age Class (Years)								Total No. of Plants
	o-1	1-2	2-3	3-4	4-5	5-6	6-7	> 7	
1:2	32.6	19.8	5.1	9.3	4.7	12.8	0.0	5.8	86
4:1	25.7	18.8	6.3	9.0	9.7	10.4	9.7	10.4	144
7:2	26.2	11.9	4.8	16.7	9.5	23.8	2.4	4.8	42
8:3	28.8	13.5	11.5	9.6	23.1	13.5	0.0	NR	52
8B:4	28.8	19.2	5.8	11.5	7.7	13.5	13.5	NR	52
Cronkley	28.6	10.2	8.2	16.3	8.2	28.6	NR	NR	49
Ave. W'bank	28.2	15.2	8.8	10.4	10.1	13.3	11.70	NR	
Ave. Overall	28.2	16.7	8.7	11.1	9.9	25.5	(NR)	(NR)	
Approx. Calc. * Figures	27	20	14	11	8	6	4	10	

In those quadrats where records are for less than 7 years, the oldest age-group includes all plants over that age.

* Based on constant recruitment and 27% annual mortality.

a quadrat is known. In one quadrat (8:3) the age of all plants is now known, and in the remainder a high proportion are of known-age. Age structures for each site, and for the total sample are presented in Fig. 5.3 and Table 5.6b together with a "model" population with constant recruitment and 27% annual mortality. These age structures generally are of the type that one would expect from a healthy population of a short-lived perennial, although there are considerable variations between sites and differences from the standard, reflecting variations in mortality and recruitment over the period during which the population was formed. Overall, the distribution of the population sample is strikingly similar to the calculated model.

5.4.6 Mortality recording.

Distinction has been made during the fieldwork for this study between two types of mortality:

a. Plants which were seen to be dead, or more or less dead, at some stage before they disappeared. ("Dead").

b. Plants which were present at one recording but of which there was no trace at the next. ("Gone").

In the latter case, plants were tentatively assumed to have been removed by sheep (on Widdybank Fell) or rabbits. Plants were unlikely to have died and rotted away between recordings, although it is possible that the remains of a plant recorded as "gone" could have been overlooked in one recording, especially if carried out in bad weather. The distinction was made because it was felt that an indication of the loss of rosettes due to sheep-grazing could thus be gained. Doody (1975) records that sheep teeth-marks had been observed on rosettes, and that there was a good degree of correlation between the percentage of mortalities recorded as "gone" and the level of sheep-grazing. For the purposes of all mortality calculations, the two types of mortality have, of

Gentiana verna

Table 5.7

Proportion of mortalities recorded as "gone"

Site	1973		1974		1975		Site averages	
	No. gone	% gone	No. gone	% gone	No. gone	% gone		
1:2	9/28	32%	21/28	75%	18/20	90%	48/76	63%
4:2	24/39	61½%	37/47	78½%	43/47	91½%	104/133	78%
7:2	2/15	13%	10/16	62½%	9/11	82%	21/42	50%
8:3	0/1	0%	16/18	89%	6/9	67%	22/28	79%
8B:4	3/5	60%	6/10	60%	17/22	77%	26/37	70%
Cronkley 10	8/14	57%	18/20	90%	12/16	75%	38/50	76%
Averages	46/102	46%	108/139	77.7%	105/125	84%		

N.B. "% gone" is % of mortalities recorded as gone.

course, been regarded as equivalent, and treated together. The proportion of deaths recorded as "gone" is shown in Table 5.7.

5.4.7 Seasonal mortality.

As indicated under Population flux (5.3), over the whole period 1969-1975 there was no significant difference in mortality between any season. Mortalities were almost exactly the same in each period of the year. Table 5.8 shows the detailed mortality rates in each site over the period 1972-1975, and analysis indicates that there are no significant differences between sites. Mortality amongst <u>Gentiana</u> rosettes is apparently constant throughout the year, in contrast to <u>Polygala</u> (sect. 4.3) where it was found to be considerably higher in the winter period.

5.5 Recruitment.

Within the sites studied, recruitment to the gentian population was almost exclusively confined to vegetatively-produced rosettes. Only 3 seedlings were recorded in one quadrat during the whole period, and the contribution of seed-derived individuals to the numbers in the population is not considered here.

5.5.1 Annual recruitment.

The levels of recruitment, shown as new rosettes per established plant, are displayed in Table 5.9, for each site over the period 1972-1975. Doody (1975) presents comparable figures for each site for the years 1969-1972, and his figures are quoted below, for comparison, as averages only:-

1969 : 0.43
1970 : 0.98
1971 : 0.43
1972 : 0.34

1:2 : 0.66
4:2 : 0.42
7:2 : 0.53
8:3 : 0.73
8B:4 : 0.45
Cronkley : 0.45

Over the period 1972-1975, the average rate of recruitment was

Gentiana verna

Table 5.8

Seasonal mortality

Mortality Period *	Sites 1:2	 4:2	 7:2	 8:3	 8B:4	 Cronkley	Seasonal Averages
Autumn 1972-Spring 1973	0.12	0.04	0.12	0.00	0.02	0.09	0.09
Summer 1973	0.00	0.01	0.00	0.02	0.06	0.00	0.01
Autumn 1973	0.14	0.14	0.04	0.00	0.00	0.05	0.08
Spring 1974	0.13	0.05	0.22	0.09	0.02	0.05	0.07
Summer 1974	0.12	0.19	0.02	0.00	0.11	0.00	0.10
Autumn 1974	0.06	0.01	0.02	0.24	0.02	0.24	0.07
Spring 1975	0.06	0.10	0.12	0.04	0.11	0.17	0.09
Summer 1975	0.14	0.00	0.00	0.14	0.00	0.00	0.04
Autumn 1975	0.01	0.12	0.05	0.00	0.19	0.00	0.08

Notes: Mortality is calculated relative to the number of plants at the start of the interval.

* The date represents the end of the interval, and the mortality opposite each row refers to the period between that date and the preceding one.

0.27 new rosettes per plant per year. Although Doody (1975) does not quote an average value for the period 1969-1972, it is clear that recruitment was at a considerably higher rate during that time, than during the period 1972-1975. The average recruitment calculated over the period 1970-1975 is 0.32 rosettes per established plant per year.

Analysis of Table 5.9 indicates that there are no significant differences between years, but that there are significant differences between sites. Further examination of the data shows that 1:2 has a significantly higher recruitment than average (P 0.01), but that there are no significant differences between other sites.

5.5.2 Seasonal recruitment.

Recruitment of new Gentiana rosettes continued throughout the year, at least to the extent that new rosettes appeared between the October record and the April/May record. A broad χ^2 analysis of the figures given in Table 5.1 for all the additions in each season indicates that there are considerably less additions in the winter, per month, than in the rest of the year over the period 1969-1975, and that this difference was significantly less than expected ($P< 0.001$). Table 5.10 presents data for rosette recruitment during each season in each quadrat over the period 1972-1975. Analysis of variance indicates that there is seasonal difference ($P<0.01$) and that the winter recruitment differs from those for the two summer periods. This is hardly surprising, although the difference is by no means as clear-cut as might be expected, perhaps because the recording times were not exactly at the beginning and end of the growing season in all years.

5.6 Reproductive performance.

5.6.1 Although a large amount of data has been collected on the flowering performance of Gentiana verna, it should be noted that

Gentiana verna

Table 5.9

Annual recruitment.

Year	Sites						
	1:2	4:2	7:2	8:3	8B:4	Cronkley	Totals
Aut.1972-Aut.1973	0.41	0.16	0.22	0.41	0.19	0.22	0.24
Aut.1973-Aut.1974	0.39	0.23	0.21	0.20	0.20	0.12	0.23
Aut.1974-Aut.1975	0.39	0.27	0.28	0.35	0.31	0.30	0.31
Site averages	0.40	0.22	0.24	0.32	0.23	0.21	0.27

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Table 5.10

Seasonal recruitment

Season	Sites						
	1:2	4:2	7:2	8:3	8B:4	Cronkley	Aves.
Aut.72 - Spr.73	0.00	0.01	0.02	0.07	0.02	0.09	0.03
- Summer 1973	0.03	0.05	0.11	0.25	0.06	0.03	0.07
- Autumn 1973	0.37	0.09	0.06	0.04	0.10	0.02	0.11
- Spring 1974	0.02	0.03	0.22	0.03	0.02	0.01	0.02
- Summer 1974	0.15	0.17	0.13	0.00	0.16	0.00	0.11
- Autumn 1974	0.21	0.02	0.02	0.14	0.00	0.10	0.07
- Spring 1975	0.02	0.06	0.04	0.00	0.05	0.12	0.05
- Summer 1975	0.24	0.02	0.00	0.19	0.06	0.00	0.09
- Autumn 1975	0.12	0.11	0.10	0.16	0.13	0.07	0.11

flowering is unimportant, under present conditions, in the annual reproduction of the species on Widdybank Fell (although its possible role in the long term survival of the species is discussed later). No fertile capsules have matured, during the period of this study, in any of the marked sites, and only 3 seedlings (recorded together in 1974) have ever been observed. Ripe capsules may be produced on these Fells, although they are rare, and are only normally found in areas where sheep do not graze, e.g. in artificial exclosures or amongst heather. The following figures and conclusions should therefore be viewed in this light.

5.6.2 Age at flowering, and fate of flowering individuals.

An analysis of the age at which rosettes first flower, if they flower, is presented in Table 5.11. Only the data for 1969 and 1970 additions are presented, to avoid bias towards those plants which flower when young. The data for these two years have been pooled because there are no records for individuals flowering after 4-5 years for the first time. One surprising feature is the paucity of individuals that have been followed from 'birth' through to flowering. Of the 329 additions recorded on Widdybank in 1969 and 1970, 29 flowered (8.8%), 239 died without flowering (72.6%) and 61 were recorded for over 5 years without flowering (18.6%).

Over 50% of plants that flower do so when aged 1-2 years, with smaller, more or less equal amounts (10-14%) in other age groups up to 5 years. No plants have been recorded as flowering for the first time when over 5 years old. The individual quadrats show more or less the same pattern, all with a peak of numbers at age 1-2 years.

Plants that have flowered face varied fates (see Table 5.12). Although it is sometimes stated that <u>Gentiana verna</u> normally dies soon after flowering, the results from this study indicate that

Gentiana verna

Table 5.11

Reproductive performance. Ages at first flowering, or length of time recorded without flowering.

Age at first flowering (years) *	Sites						
	1:2	4:2	7:2	8:3	8B:4	Cronkley	Widdybank Total
0-1	2	0	3	0	0	0	4 (13.8%)
1-2	3	4	0	0	8	2	15 (51.7%)
2-3	3	1	0	0	0	0	4 (13.8%)
3-4	2	0	0	0	1	0	3 (10.3%)
4-5	1	2	0	0	0	0	3 (10.3%)
5-6	0	0	0	0	0	0	
No. dying without flowering	69	88	39	22	21	14	239
No. recorded over 5 years from birth without flowering	11	28	11	7	4	3	61

* Using data from 1969 and 1970 additions.

On Widdybank sites, out of those recorded, 72.6% died without flowering, 18.6% lived through the study period without flowering, and 8.8% flowered. For Cronkley, the comparable figures are: 73.6%, 15.8% and 10.6%.

Gentiana verna

Table 5.12

Analysis of the fate of plants that flower.

	Site		
	Widdybank sites	Cronkley	Total
Number of plants that die within year of first flowering, and as percentage of all flowering individuals	50 45%	7 44%	57 45%
Number and percentage of plants that flower and survive to a further year	62 55%	9 56%	71 55%
Number of plants that flower twice, and percentage	15 13%	0 0%	15 12%
Number of plants that flower three times	0	0	0
Number of plants that flower again in the following year	11	0	11
- or the second year after	4	0	4
- or the third year after	0	0	0
Number of plants that die within the year of second flowering, and as percentage of those that flower twice.	7 47%	0 0%	7 47%

only 45% of rosettes die within their year of first flowering, with the remaining 55% (71 plants) surviving at least to the following year, and possibly flowering again.

Of the 128 recorded flowering individuals, 15 were recorded as flowering twice (12%), with 11 of these flowering again in the year after their first flowering, and 4 in the year after that. 7 out of 15 (47%) then died within their year of second flowering, the remainder (53%) surviving to at least a further year, although no plants were recorded as flowering three times or more. Some aspects of these figures are surprising, especially the large numbers of plants (73%) that die without flowering, or survive for over 5 years without flowering (19%). The possible significance of this is discussed later(in 5.7). It would appear that flowering does increase the risk of death, since 45-47% of plants die within the year of flowering, compared to the normal annual mortality of all plants of 27%, although over half survive to subsequent years. Probably the risk of death would be increased if capsules were produced, due to the greater drain on the plant's resources.

5.6.3 Flowering percentage and reproductive potential.

<u>Gentiana verna</u> flowers each year in spring, usually during May in the study area, and each rosette normally produces a single blue flower, although up to 3 flowers per rosette have been observed on Widdybank Fell, and greater numbers elsewhere. Over all sites and all years, an average of just under 7% of rosettes flowered each year. Of those recorded in quadrats, none produced ripe fruit in the period 1972-1975, although Doody (1975) records that a few capsules were produced in plot 10 on Cronkley Fell in 1970. The average number of seeds per capsule collected from exclosures is 161 (see Table 5.13), so the average reproductive

Gentiana verna

Table 5.13

Seed production

	Seeds per capsule	
Year	Widdybank Fell	Cronkley Fell
1970	143 ± 11	182 ± 30
1971	132 ± 13	
1972	182 ± 11	
1973	127 ± 52	
1974	205 ± 56	
1975	126 ± 75	
Ave.	161	

potential of the gentian on Widdybank Fell might be 1127 seeds/ 100 plants per annum if all capsules reached maturity, and assuming that flowering percentage remained the same under such conditions. Taking the average density of rosettes, calculated from plot data to be 109 M^{-2}, then the average potential seed production of Gentiana on Widdybank is 1228 seeds/M^{-2}/year.

Table 5.14 shows percentage individuals producing flowers (where number of flowers per flowering plant = 1 throughout the whole period) in each site in each year. The data were analysed as explained in section 3.5.7 using transformed data, with a "missing plot" figure calculated for Cronkley 1969, and applying Least significant difference and Least significant range (where Q^{6}_{30} or Q^{5}_{30} was the multiplying factor, for year differences and site differences respectively) tests. (Fisher, 1954). The initial analysis indicated that there were significant differences between years and between sites, ($P< 0.01$) with no significant interaction between them. Further analysis showed that Site 8B:4 had a significantly higher flowering percentage than all others ($P<0.001$) and that 1:2 was significantly higher than all others (except 8B:4) ($P< 0.001$). Sites 7:2 and 8:3 were significantly lower than average (P 0.01) although not from each other nor from 4:2.

Amongst years, 1975 was significantly lower than all others ($P< 0.001$) and 1971 was significantly lower than the remaining years. 1970 and 1973 were significantly higher than all other years except 1969 ($P< 0.001$), which was not in itself significantly different from average.

In summary, 8B:4 had the highest flowering percentage, followed by 1:2, while 7:2 and 8:3 had significantly lower than average flowering percentages. Cronkley and 4:2 were neither significantly higher nor lower than average.

Gentiana verna

Table 5.14

Annual flower production. Percentages of plants producing flowers.

Years	Sites						
	1:2	4:2	7:2	8:3	8B:4	Cronkley	Averages
1969	12.5	7.0	3.5	1.6	18.8	NR	8.8
1970	9.5	5.4	7.0	4.8	14.9	7.8	8.2
1971	8.5	2.7	0.0	2.1	8.3	11.1	5.4
1972	14.4	4.7	1.5	1.9	13.3	6.3	7.6
1973	7.3	8.5	8.2	6.3	17.5	2.9	8.7
1974	7.6	5.2	6.0	2.9	21.3	0.0	7.6
1975	2.1	0.0	0.0	0.8	6.9	2.5	1.8
Site aves.	9.1	4.8	3.7	2.9	14.5	5.2	6.83

1975 was the worst year for flowering, followed by 1971, while 1970 and 1973 were the best. 1969 had a high average percentage but was not significantly higher than average. The remaining years did not differ significantly from average. The possible significance of these differences is discussed later (in 5.8).

5.7 Life cycle and Reproductive strategy.

In summary, Gentiana verna is a short-lived perennial with an average life expectancy of about 3 years, and an average annual mortality of 27%. Approximately 7% of rosettes flower each year, on average, with each rosette normally producing a single flower, which rarely develops into a capsule under the conditions prevailing in the study area. Rosettes may very occasionally flower within their first year, but normally flower in their second or third years. They rarely flower more than once, although many survive for long periods after flowering. Pollination has not been studied in detail, and relatively little is known of the pollinators. Bombus spp. have been observed visiting flowers in the normal manner on still fine days, when these occur. In addition, bees, and possibly other insects obtain nectar "illegally" by biting through the corolla tube at the base, and the results of this can often be observed. Despite the problems of poor weather, scarcity of pollinators, and "illegal" entry, it is clear that many capsules, with fertile seeds, do develop in ungrazed areas. Elkington (1963) records that G. verna is self-compatible, and although spontaneous self-pollination has not been observed under experimental conditions, it may take place in the wild.

Under these conditions, the normal mode of reproduction is by the production of fine underground stolons terminating in rosettes which have been recorded as appearing up to 25cms from the nearest plant, and which may therefore gradually serve to colonise new ground. These rosettes are produced almost throughout the year, but especially in warmer damper periods. The young rosette then has as much chance of survival as an adult plant, and, in fact, all ages of plant seem to have a similar chance of survival (i.e. mortality is age-independent). Flowering individuals are more likely to die than non-flowering ones (45%, compared to 27%) and possibly more plants would die in their year of flowering if they were allowed to produce ripe fruits which would diminish their reserves further.

From the few capsules that are produced, in particular protected sites, the reproductive potential is thought to be reasonably high (c. 1100 seeds/100 plants/annum), but only a very few seedlings have been recorded in the study area. Within the 7 years of this study, to 1975, only 3 seedlings have been recorded in the permanent quadrats, all in one quadrat in 1974. The seed must have been produced outside the quadrat, unless it had lain dormant for a long period of years.

Although clearly not of importance in directly determining the numbers of individuals on the Teesdale Fells, sexual reproduction may be of importance in occasionally producing new genetic recombinants which may be more suited to certain conditions than the present clones. Additionally, clonal material in many species (although there is no evidence for this in <u>Gentiana verna</u>) eventually loses its vigour, and new clones from seedlings would therefore help to maintain the population.

The method of vegetative growth is clearly successful and well-suited to the conditions in the study area. The populations are maintained despite quite large annual losses of plants, and, in some quadrats, numbers have increased over the 6 years to 1975.

The relationship between Gentiana verna and the grazing sheep (or rabbits) is complex and by no means fully clear. The sheep probably assist the survival of Gentiana on these fells to an extent by keeping the vegetation short, and altering its composition to those species able to survive grazing. The Gentiana thrives, often at quite high densities (e.g. c. 170 rosettes/M^{-2} in one quadrat) in a grazed plagioclimax. In an exclosure on Widdybank Fell set up in 1969, Gentiana was at first very successful in flowering, and large numbers of capsules were produced. Since that time, the numbers of rosettes, flowering individuals and ripe capsules have all decreased (Doody 1975, and subjective assessment) as the growth of other vegetation, especially Festuca ovina has increased. To this extent, sheep probably assist the species by extending the range of habitat that it can colonise, and by allowing it to succeed within this. In opposition, sheep may regularly remove whole plants and probably damage others irrevocably, and almost totally prevent seed production.

The very high proportion of plants that die without ever flowering, or have lived for over 5 years without flowering (92%, together) is remarkable. There may be 2 reasons for this. Firstly, grazing may directly prevent a proportion of plants from achieving the state of vigour that they require to produce flowers. There is reasonable general evidence to support this, from horticultural experience in particular, and definite evidence that full defoliation may reduce or entirely prevent seed formation in some species (e.g. Rockwood 1974), whilst partial defoliation after anthesis may considerably reduce seed size (e.g. Maun and Cavers, 1971). It is likely, therefore, although by no means definitely shown by this study, that the general reproductive performance of the Gentiana will be impaired by continuous grazing through the growing season.

Secondly, there is probably an overall selection pressure to reduce the flowering percentage on the Fell, by selection of non-floriferous clones. This is suggested because:

1. Flowering plants probably produce less new rosettes than non-flowering ones through diversion of resources to flowering, and, since they will not normally produce seeds, they will have less offspring overall;
2. Plants that flower, as previously shown, are likely to die earlier than non-flowering ones, and are likely therefore to have less time to produce new rosettes;
3. Flowering individuals are probably more likely to be removed whole, possibly together with any new stolons, by grazing sheep since they are taller and more conspicuous, and a small experiment indicated that this removal does not stimulate increased rosette production by the remaining rootstock.

In other words, there is no immediate advantage to the population, under present conditions, to flower, and there are probable positive disadvantages. There would appear, therefore, to be quite strong pressure to reduce floriferous clones, and little to favour them.

If this mechanism is operating, it is probable that it will already have had considerable effect, and this may be the underlying cause of some of the observed differences in flowering percentage between different sites. It may also help to explain the obviously greater flowering percentage of the rosettes at a little-grazed site at Langdon Beck, not far away. Further experimental and perturbation studies should be made to analyse the situation more fully. It is difficult to gauge the likely speed of change, but - with the short generation time of <u>Gentiana</u> -

it may be sufficiently rapid to be taken into account in consideration of future management. Brougham and Harris (1967), for example, showed that genetic changes occurred in strains of Lolium within a few months of sowing, under particular grazing regimes, and Charles (1964, 1968) has shown the rapidity of adaptation of red and white clover and grass populations to different management regimes.

Although the gentian can clearly survive with a low flowering percentage in the site area, its prime attraction is its flower and management should possibly be directed at ensuring more than the survival of its rosettes.

Chapter Six

Viola rupestris

6.1 Introduction.

Viola rupestris, the Teesdale Violet, is an extremely rare native of Britain, confined, within Britain, to a few sites in Northern England in open limestone vegetation. It is listed by Perring and Farrell (1977) as an endangered species, and is recorded from only 7 10Km squares in England (Bradshaw and Doody, in press). Within Teesdale, it is confined to Widdybank Fell, along the narrow band of sugar limestone soil, growing in a range of communities from closed short grassland to open eroding edges, although never amongst dwarf shrubs. It is a small perennial rosulate herb, which loses its leaves in winter, but which is apparently relatively long-lived. Flowering, in common with other members of the genus Viola, involves the production of both open (chasmogamous) and closed (cleistogamous) flowers, and the relative importance of these two is determined to an extent by habitat.

For the purposes of this study, the definition of the "unit of reproduction" has followed that given by Doody (1975) in order that results over the whole period will be comparable. He describes the production of short lateral branches terminating in rosettes, which do not appear to root independently, but whose connections with the parent plant are not always distinguishable in the field without causing damage, illustrating some of the problems discussed by Harper (1967). Doody therefore defines the individual or 'unit of reproduction' as "any rosette which arises from a seed or underground stem".

6.2 The recording sites.

Viola rupestris occurs only on Widdybank Fell within the Upper Teesdale area. Sites were selected in four main areas on the fell, one (site 2) within a few metres of the reservoir edge (TWM), one about 100 metres from TWM (site 3), one about 300 metres from the reservoir edge (site 6) and the other over 500 metres from TWM (site 9). Within these categories of distance from the reservoir, the sites fell broadly into two main vegetation types; those at 3 and 6 lay in closed turf, while those at 2 and at 9 lay in more open vegetation.

Quadrat 2:2 was four metres long, running down a gentle west facing slope towards the reservoir edge; the vegetation was generally disturbed, by mole runs and frost-heaving, and there were considerable numbers of small open areas. The dominant species was Festuca ovina in a rather depauperate state, with Sesleria caerulea, Koeleria gracilis, Briza media, Carex flacca, and Minuartia verna also present, amongst others. This quadrat was less affected by the blown sand described for 2:3 below.

Quadrat 2:3 was one metre long, on a short ledge of vegetation amongst eroding sugar limestone edges, only a few metres from the reservoir edge. Sesleria caerulea and Festuca ovina were the dominant species, and Doody (1975) records that approximately 13% of the quadrat was without vegetation cover in 1972. In 1973-74, considerable quantities of sand from the sugar limestone beach nearby was blown on to the adjacent bank, partially covering the vegetation, and making some plants difficult to refind. This gradually cleared or settled, and most plants were re-located.

Quadrat 3:2 was 2 metres long and lay on a steep south-west-facing slope amongst closed grazed turf. The sward was dominated by Festuca ovina and Sesleria, with lesser amounts of Kobresia, Carex capillaris and Plantago maritima, amongst others.

Quadrat 3:4, 2 metres long, lay close to 3:2, but in rather more open vegetation, for which Doody (1975) presents a map of a sample metre. The turf was dominated by Sesleria and Festuca ovina with lesser amounts of Kobresia and Plantago maritima amongst others

Quadrat 6:2 was 5 metres long, running down a west-facing slope, where the vegetation consisted of a closed turf, dominated by Festuca ovina and Sesleria, with Kobresia and Primula farinosa (for which the quadrat was also recorded) amongst others. The density of Violets was low (17 M^{-2}).

Quadrat 9:2 was 2 metres long, and lay on an eroding sugar limestone edge. During the period of recording a number of plants "moved" out of the quadrat, over this eroding edge. The density of Viola rosettes was high, amongst an open vegetation dominated by Sesleria and Festuca ovina.

Quadrat 9:3, one metre long, lay in stony open vegetation, with almost 50% bare ground, and large quantities of mosses and lichens (in particular Tortella tortuosa and Cladonia spp.). It was flat and apparently very dry.

Five sample sites were established, one at each of sites 2 and 3, and one associated with each of quadrats 6:2, 9:2 and 9:3, as explained in 3.2.

6.3 Population flux.

Figs. 6.1 and 6.2 show the changes in numbers that have taken place over the period of recording. Over the whole period, the number of plants has increased in 5 quadrats out of 7, and decreased slightly in 2. In 6:2, the numbers decreased by 1, and in 9:3 by 9 (about 16%), although they do not seem to be part of a trend to decrease, but rather that the Autumn 1975 figure was a chance lower number; for example, the highest recorded figure in 9:3 was in summer and autumn 1974, only a year before the final record. In contrast, most other quadrats showed a tendency to increase, with only infrequent returns to the original low numbers. The overall

FIG 6.1. VIOLA RUPESTRIS

POPULATION FLUX IN FOUR QUADRATS, 1968-1975.

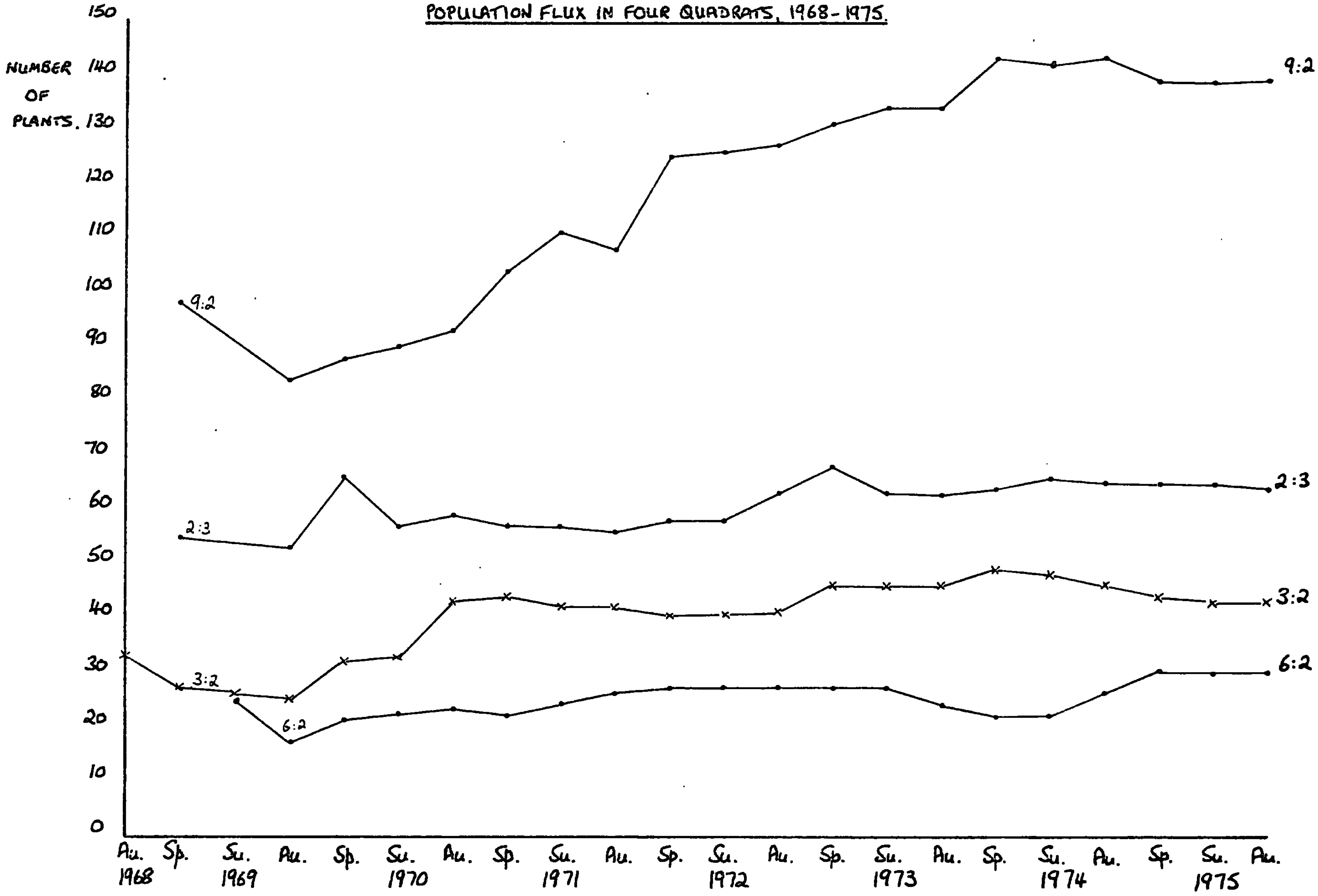
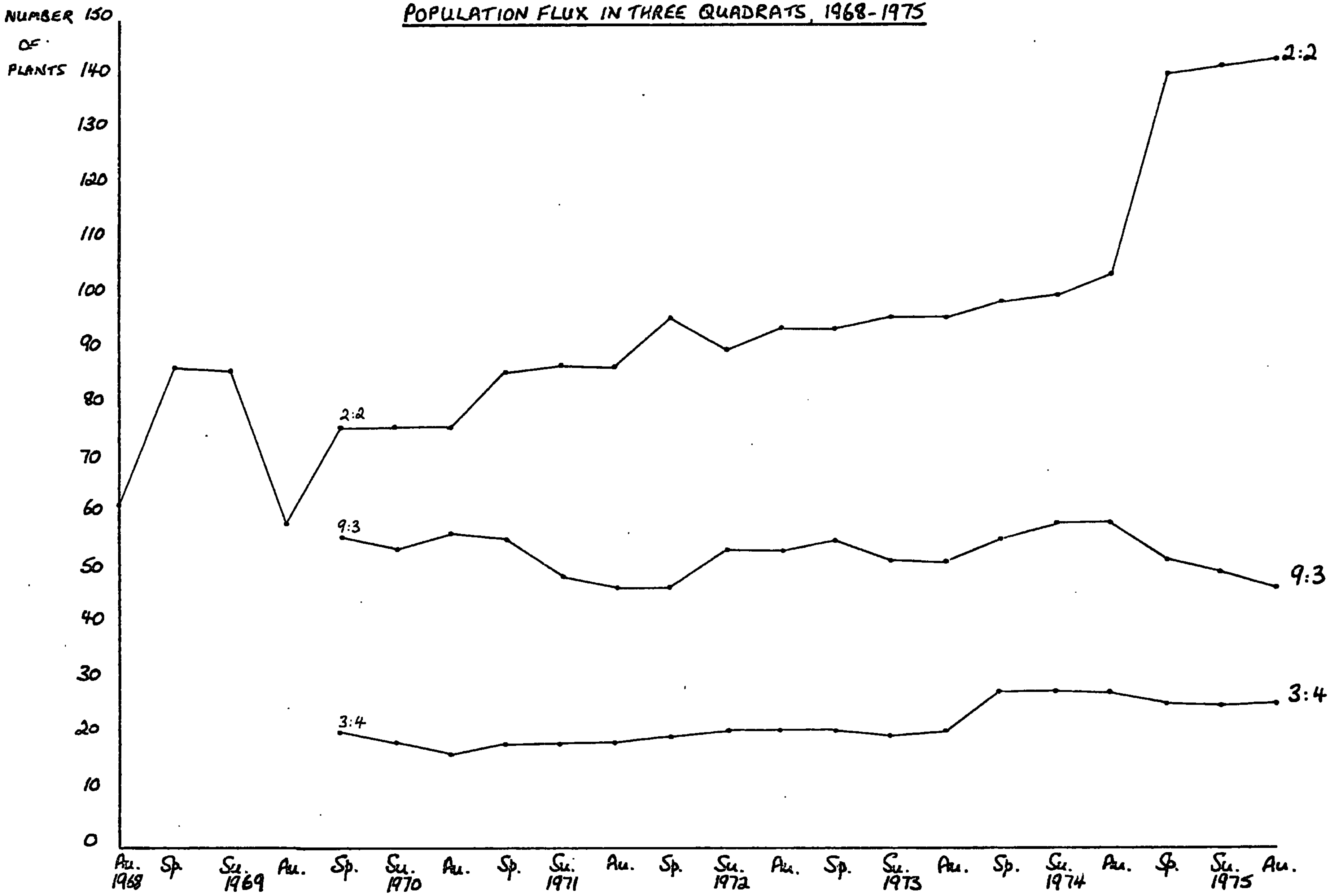


FIG. 6.2. VIOLA RUPESTRIS

POPULATION FLUX IN THREE QUADRATS, 1968-1975



Viola rupestris

Table 6.1

Additions and mortalities in all permanent plots.

Season	Additions			Mortalities			Change in pop. nos. + or -	Population numbers
	Seed.	Veg.	Tot.	Seed.	Other	Total		
Aut. 1968								93(2 quads)
Spr. 1969	56	0	56					218(4 quads)
Sum. 1969	1	2	3					Incomplete
Aut. 1969	0	20	20					212(5 quads)
Spr. 1970	38	29	67					354
Sum. 1970	0	20	20	2	26	28	-8	346
Aut. 1970	0	31	31	2	12	14	+17	363
Spr. 1971	28	14	42	2	20	22	+20	383
Sum. 1971	0	14	14	1	12	13	+1	384
Aut. 1971	0	8	8	0	12	12	-4	380
Spr. 1972	34	13	47	3	19	22	+25	405
Sum. 1972	0	15	15	1	11	12	+3	408
Aut. 1972	1	20	21	0	9	9	+12	420
Spr. 1973	31	6	37	12	24	36	+1	421
Sum. 1973	2	8	10	0	13	13	-3	418
Aut. 1973	10	4	14	0	6	6	+8	426
Spr. 1974	16	9	25	2	19	21	+4	430
Sum. 1974	0	10	10	0	8	8	+2	432
Aut. 1974	7	6	13	0	0	0	+13	445
Spr. 1975	35	18	53	3	34	37	+16	461
Sum. 1975	10	2	12	1	5	6	+6	467
Aut. 1975	0	4	4	1	5	6	-2	465
Totals	269	253	522	30	235	265		

number of plants, in all quadrats, has increased since spring 1970 (the first time that all 7 quadrats were recorded) by 24%, from 354 to 465 individuals. The lowest figure, 346, was recorded in Summer 1970, and there has been a steady increase since then.

The mechanics of the population changes are shown in Table 6.1. Overall, additions have been more or less equally due to seedlings and vegetative recruitment, with overall additions exceeding mortalities in 13 out of 17 recording periods. Mortality records are incomplete for the period preceding the summer 1970 "trough", but as recruitment was high in the preceding period, presumably the decline was due to unusually high mortality.

6.4 Mortality rates and Life expectancies.

6.4.1 In general, the turnover rate of Viola rupestris individuals was low, with about 14-15% of plants being lost each year, on average, although considerable variation exists between years and between sites.

6.4.2 Age-specific mortality.

Doody (1975), by inspection of semi-logarithmic decay curves of original mixed-age populations over the period 1968-1972 concludes that mortality in Viola rupestris is independent of age. A different indication of the variation of mortality rate with age may be gained by looking at the decay of cohorts of known-age. Table 6.2 shows the data for decay rate of all additions over the period 1969-1975 with reference to their age. As discussed in 3.5.2., the sample size necessarily decreases with increasing age, in addition to the decrease caused by mortality, with a corresponding increase in the variance of each mortality estimate.

Table 6.2

Age-specific mortality. Autumn figures.

No. at risk	357	224	154	82	49	21
No. dying	86	28	19	3	4	0
Mortality	0.241	0.125	0.123	0.037	0.082	0.000
Age Class (yrs.)	0-1	1-2	2-3	3-4	4-5	5-6

If the cohorts decayed exponentially, the best estimate of the decay rate between each age class would be 0.158. Preliminary inspection of the data indicates that they do not fit this pattern, with the 0-1 decay being considerably greater than average, and all remaining age classes being lower than average. A χ^2 analysis indicates that there is a high degree of difference from the expected pattern ($\chi^2_5 = 36.87$ $P < 0.001$), and the 0-1 mortality rate is shown to be significantly higher than expected ($P < 0.001$). Although all other age-classes show lower mortality than expected, the numbers are too small relative to the first age class for the differences to show up as significant. The numbers used exclude seedlings or vegetative additions until their first autumn, and thus the early age mortality includes the death of seedlings over their first winter.

Mortality for age-classes excluding seedlings until after their first winter was therefore examined over annual periods from spring to spring, as explained in 3.5.4. Table 6.3 shows mortality of each age class, for all years totalled, in this way.

Table 6.3

Age-specific mortality. Spring figures.

No. at risk	254	159	90	50	21
No. dying	50	13	9	5	21
Mortality	0.1969	0.0818	0.1000	0.1000	0.0000
Age Class (yrs.)	0-1	1-2	2-3	3-4	4-5

If an exponential curve was fitted to the data on the best estimate, the decay rate between each would be 0.1341. Again, inspection indicates that the data does not fit this pattern. χ^2 analysis indicates that there is a significant difference from expected exponential decay ($\chi^2_4 = 17.02$ $P<0.01$), and mortality from 0-1 was higher than expected ($P<0.01$) while mortality from 1-2 was lower than expected ($P<0.01$). The indications are, therefore, that mortality is higher in the first 18 months or so of life, and then lower, and that early increased mortality is not caused simply by seedlings dying during or before their first winter.

To understand the contribution of seedling mortality to this pattern, mortality of seedlings over their first year, separated into 2 six-month periods was investigated. Seedlings from spring only were examined, and the results are shown in Table 6.4 below.

Table 6.4

Seedling mortality during the first year of life.

	No. of seedlings germinating, Spring	No. remaining at Autumn	No. remaining at following Spring
	302	268	225
M:		0.1126	0.1605

Records from all years pooled.

The annual mortality rate over this period is therefore 0.255, and the corresponding expected 6-monthly mortality rates, calculated as explained in 3.5.5, would be 0.14. Thus, mortality of seedlings is considerably higher over their first year than the average annual rate for adults excluding seedlings (0.255 cf. 0.134), and within that first year, a greater loss occurs over the second six months, i.e. the winter period. This contrasts with the findings for <u>Polygala amarella</u> that seedlings survive as well as adults.

Clearly, therefore, much of the high loss in the 0-1 year class in Table 6.2 was due to overwinter seedling mortality, but the indications from Table 6.3 are that mortality continues to be higher for a further year. More records are required before the rate of mortality in older age-classes can be estimated, although the indications are that increasing age decreases the risk of death. Assuming that mortality rate is age independent, for the purposes of comparison, half-lives are calculated for mixed-age populations and subsequent seedling and vegetative additions up to 1971, although the figures shown in Tables 6.2 and 6.3 indicate that this may not be entirely appropriate as a way of describing the decay of Violet plants. The calculated half-lives are shown in Table 6.5. The general indications from this are that plants in 9:2 and 2:3 are the longest-lived, that seedling additions may live longer than vegetative additions, and that cohorts with different times of origin have very different half-lives, even within the same quadrat. The half-lives of the seedling cohorts are likely to be underestimates in view of their high initial mortality.

On the basis that ½-life is roughly ¼ of the total expected turnover time, the turnover of plants in a <u>Viola rupestris</u> plot would be expected to be complete in about 20-40 years, depending on the site.

<u>Viola rupestris</u>

Table 6.5

Half-lives of mixed age populations and
vegetative and seedling cohorts (in yrs.)

	Site							
	2:2	2:3	3:2	3:4	6:2	9:2	All plots	
Mixed age pop.	5.78	9.24	7.70	7.97	5.33	10.00	5.00	8.66
<u>Seedling adds.</u>								
Spring 1969	2.24	4.30	NR	NR	NR	5.13	NR	-
Spring 1970	6.30	5.50	1.78			3.47		-
Spring 1971	3.85		4.62	NR	NR	11.95	NR	6.24
Spring 1972	7.70	8.66	1.50	NR	NR	4.08	NR	4.68
Spring 1973								4.20
<u>Vegetative adds.</u>								
Autumn 1969	4.62	3.79	6.00	NR	4.00	NR	NR	-
Spring 1970	4.95	4.47	3.46	NR	9.37	NR	NR	-
Summer 1970	4.62	5.25	6.93	NR		9.00	NR	4.56
Autumn 1970	15.75	6.93	NR	NR	NR	5.00	0.97	4.75
Spring 1971	6.30		NR	2.84	NR	0.62	NR	3.03
Summer 1971		-	NR	NR	2.25	1.96	NR	2.36
Autumn 1971	-	-	-	-	-	-	6.86	

Life expectancies at birth have been calculated for individuals in each site, separating seedling additions from vegetative. Table 6.6 shows the calculated values together with the sample size available for each calculation; some of the wider variations are probably due to small sample size which may give misleading effects. The overall variability of the estimates makes the data difficult to interpret, although the indications are that seedling additions may be slightly longer-lived than vegetative additions, and that plants in 9:2 probably have the greatest life expectancy (ignoring the high figures for seedlings or vegetative additions in 6:2 and 3:4 which are based on very small samples).

6.4.3 Annual mortality.

Table 6.7 shows the annual loss of plants, excluding seedlings until after their first winter, in each *Viola* plot over the period 1969-1976. The overall annual average loss rate is 0.14, i.e. 14% of all non-seedling plants die each year. The data from Table 6.7 was analysed, as described in 3.5.4. This showed that there were significant differences between years, ($P \ll 0.001$), but not between sites, although there was a strong indication of interaction between years and sites ($P < 0.001$). Partition of the data further indicated that 1975-1976 and 1969-1970 both showed much higher mortality than expected ($P < 0.001$), while all other years were not significantly different from expected. The simple conclusion that there are no differences between sites but that there is a high degree of interaction between years and sites does not make sense; sites must be different to show this interaction. It is presumed therefore that different sites are reacting differently to given years, but that, on average, they appear the same. In other words, plants in sites do react differently to each other, on account of small-scale environmental differences, but that on

Viola rupestris

Table 6.6

Calculated life expectancies for individuals in each plot, using data from start of recording to Autumn 1975.

Plot	Seedling Additions	Vegetative Additions
2:2	4.29 (121)	10.57 (64)
3:2	6.00 (26)	8.00 (23)
2:3	6.57 (44)	7.35 (37)
3:4	7.50 (9)	17.00 (10)
6:2	19.00 (7)	6.5 (23)
9:3	7.00 (8)	7.00 (30)
9:2	11.30 (84)	5.83 (52)
All sites 1970 - 1975 Spr. Aut.	10.34 (202)	7.76 (194)

Numbers in brackets indicate the size of the sample available.

Viola rupestris

Table 6.7

Annual mortality* 1969-1976, spring records.

	Site							
Year	2:2	2:3	3:2	3:4	6:2	9:2	9:3	Yr. Aves.
1969-1970	0.33	0.13	0.26	NR	NR	0.20	NR	0.23
1970-1971	0.11	0.29	0.04	0.25	0.06	0.06	0.13	0.13
1971-1972	0.01	0.07	0.18	0.00	0.00	0.06	0.27	0.09
1972-1973	0.13	0.07	0.11	0.11	0.08	0.10	0.07	0.10
1973-1974	0.07	0.10	0.11	0.05	0.26	0.09	0.12	0.10
1974-1975	0.07	0.10	0.13	0.10	0.05	0.10	0.10	0.09
1975-1976	0.12	0.25	0.25	0.36	0.12	0.27	0.25	0.23
Site aves.	0.11	0.15	0.16	0.16	0.10	0.14	0.16	0.14

* excluding seedlings until after their first winter

average (at least in the period 1969-1976) these differences largely cancel out.

6.4.4 Seasonal mortality.

To attempt to understand some of the factors affecting mortality of Viola rosettes, mortalities have been separated into three seasons, corresponding to the periods between recording times, and the mortality in each compared. Table 6.8 shows the seasonal specific mortality in each quadrat over the period 1972-1975, adjusted as described in 3.5.5. Inspection indicates that the mortality rate is higher over the winter, and analysis of the data, including figures from spring 1971 onwards, indicates that mortality in winter is higher than expected ($P < 0.05$), while mortality in spring (July-October) is lower than expected ($P < 0.01$), and average in summer (May-July). These results contrast with the suggestion (though not demonstration) by Doody (1975) that mortality is higher in the summer 6 months of the year.

6.4.5 Age structure.

The age structure of each quadrat is shown on Fig. 6.3 together with a 'model' age-structure for a population with 14% mortality spread equally over all age-classes, (i.e. age independent mortality and constant recruitment. Neither individual quadrats nor the total population sample are closely comparable to the model structure. The age-structure reflects the mortalities and recruitments over the period during which the population was formed, but it is not an indication of the mortality rate or recruitment rate of that population, as discussed in Chapter 1. It is noticeable that there are larger numbers of plants over 5 years old than expected; 49% observed compared to 24% expected, (Table 6.8b).

It is readily observable that older Viola rupestris plants have a long woody stem-stock, and an attempt was made to find a

Viola rupestris

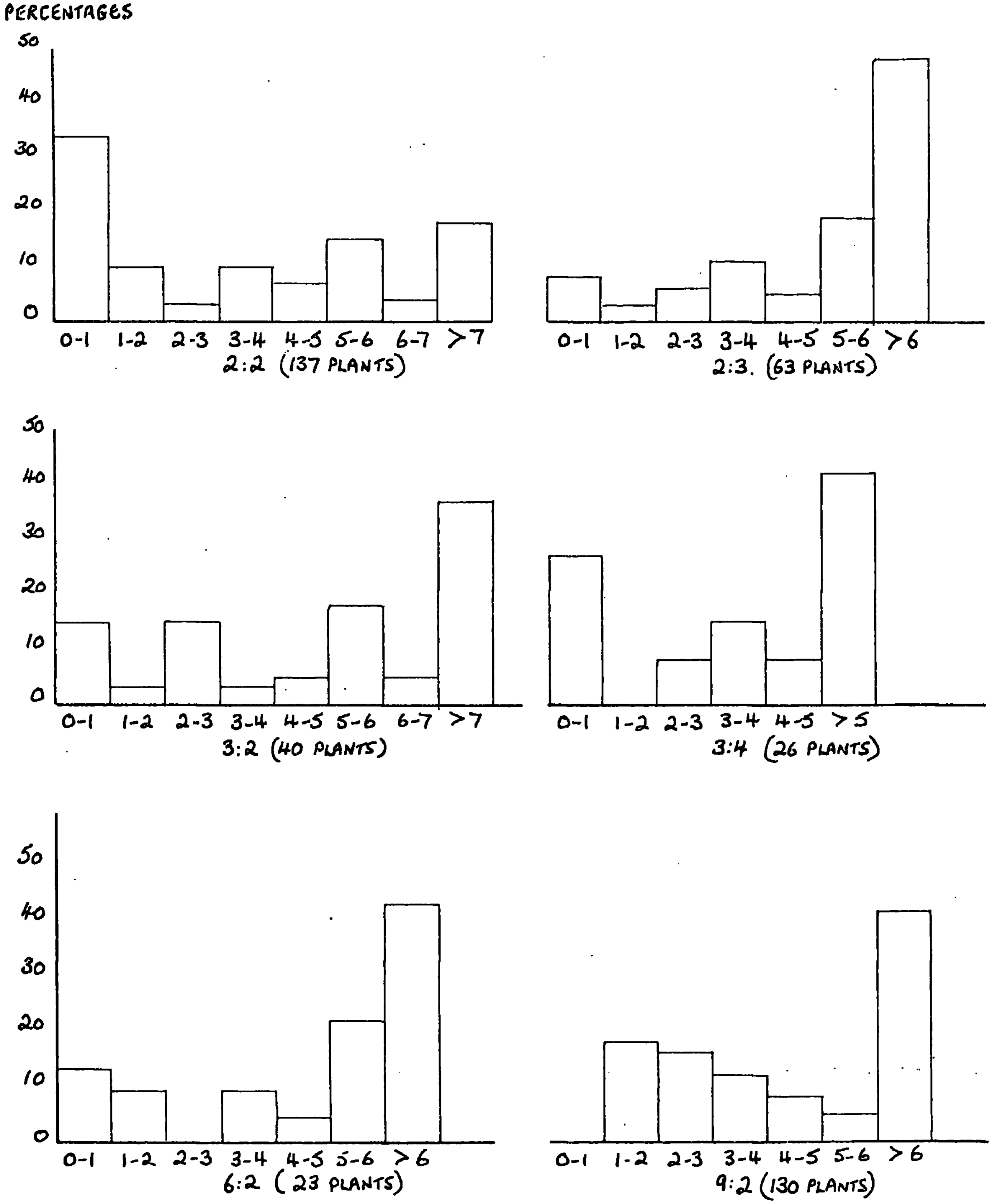
Table 6.8

Seasonal mortality.

Season	Sites 2:2	2:3	3:2	3:4	6:2	9:2	9:3	Overall Aves.
Aut. 72 - Spr. 73	0.03	0.04	0.05	0.03	0.00	0.08	0.03	0.05
Summ. 73	0.01	0.01	0.00	0.05	0.00	0.01	0.11	0.02
Aut. 73	0.01	0.00	0.02	0.00	0.11	0.00	0.00	0.01
Spr. 74	0.03	0.01	0.04	0.00	0.09	0.04	0.01	0.03
Summ. 74	0.01	0.00	0.02	0.00	0.00	0.02	0.02	0.01
Aut. 74	0.00	0.02	0.06	0.00	0.00	0.01	0.00	0.01
Spr. 75	0.04	0.04	0.02	0.06	0.00	0.03	0.05	0.04
Summ. 75	0.00	0.00	0.02	0.00	0.00	0.00	0.04	0.01
Aut. 75	0.00	0.02	0.00	0.00	0.00	0.00	0.06	0.01

FIG. 6.3 VIOLA RUPESTRIS

AGE CLASS DISTRIBUTIONS AT AUTUMN 1975



2:2 (137 PLANTS)

2:3. (63 PLANTS)

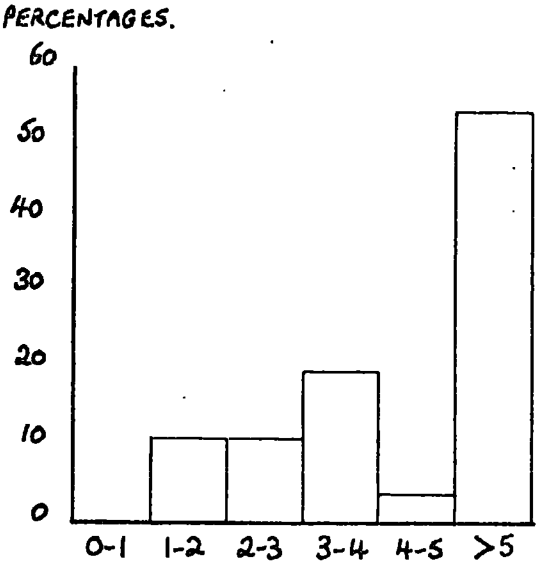
3:2 (40 PLANTS)

3:4 (26 PLANTS)

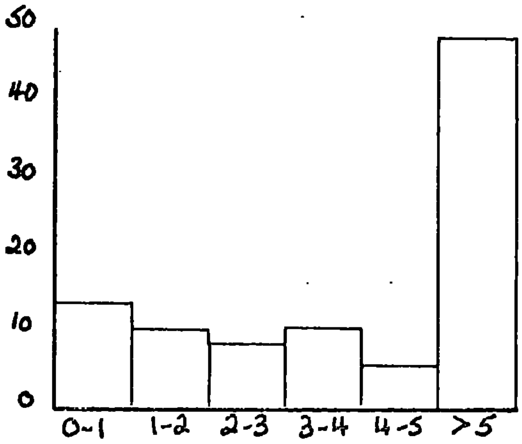
6:2 (23 PLANTS)

9:2 (130 PLANTS)

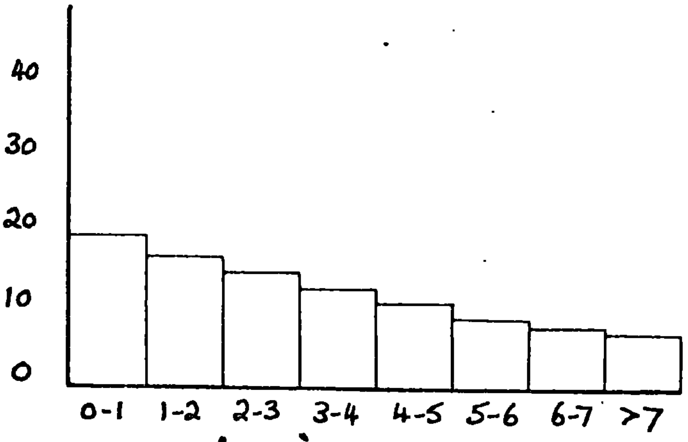
FIG. 6.3 VIOLA RUPESTRIS (cont.)



9:3 (46 PLANTS)



ALL PLOTS



"MODEL" POPULATION
14% ANNUAL MORTALITY.

Viola rupestris

Table 6.8b

Age class distribution in each quadrat, and overall, at Autumn 1975.

Plot No.	Numbers in each age class, with % below								Total nos. at Autumn 1975
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	>7	
2:2 No.	46	14	4	14	9	20	6	24 (O.P.)	137 inc. 1975 seedling
%	34	10	3	10	7	15	4	18	
2:3 No.	5	2	4	7	3	12	30 (O.P.)	NR	63
%	8	3	6	11	5	19	48		
3:2 No.	6	1	6	1	2	7	2	15 (O.P.)	40
%	15	3	15	3	5	18	5	37	
3:4 No.	7	0	2	4	2	11 (O.P.)	NR	NR	26
%	27	0	8	15	8	42			
6:2 No.	3	2	0	2	1	5	10	NR	23
%	13	9	0	9	4	22	43		
9:2 No.	0	23	21	16	10	6	54	NR	130
%	0	18	16	12	8	5	42		
9:3 No.	0	5	5	9	2	25	NR	NR	46
%	0	11	11	20	4	54			
Overall Aves.	67	47	42	53	29	86 (all quads)	102 (5 quads)	39 (2 quads)	465
%	14	10	9	11	6	19	22	8	

over 5 yrs in all quadrats = 49%

O.P. - Those remaining from the original population, and additions through the first year of recording.

NR - No records - quadrat recorded for shorter time.

reliable, repeatable, method of age determination on morphological grounds, by examination of both fresh and herbarium material. No such method was found, so the only plants of known age in this study are those that have been followed from birth.

6.5 Recruitment.

As shown in section 6.4, Viola rupestris plants are reasonably long-lived, and thus rate of recruitment need be less high than in short-lived species to maintain the population. Distinction is made here between seedling recruitment, which is the sole method of producing new independently-rooted individuals, and vegetative recruitment, as described in 6.1, where shoots develop that remain attached to their parent, but whose connections are not visible, and are therefore treated as new individuals, following Doody (1975). The relative importance of each method is discussed below (in 6.7), but are analysed here only in terms of numbers.

6.5.1 Seedling recruitment.

Table 6.9 shows the rate of recruitment of seedlings in each quadrat per established plant over the period 1973-1975. Doody gives figures for seedling recruitment over the period 1969-1972, and his average values are quoted below:

1969	0.27	2:2	0.23
		2:3	0.15
1970	0.12	3:2	0.10
		3:4	0.02
1971	0.08	6:2	0.05
		9:2	0.13
1972	0.09	9:3	0.01

No significance tests were given , although he concludes that recruitment is particularly high in 2:2, and particularly low in 3:4, 6:2, and 9:3. He also points out that germination was considerably higher in 1969 than later years, and relates this to low termperatures in the preceding winter.

Inspection of Table 6.9 indicates that site 2:2 has the highest recruitment, while 3:4, 6:2 and 9:3 have the lowest, agreeing precisely with the period 1969-1972. Analysis of the data, however, indicates that there are no significant differences between sites or between years. Overall, therefore, there are indications that site 2:2 has the highest recruitment, while sites 3:4, 6:2 and 9:3 all have low recruitment, but the differences are not strongly enough marked over the period 1973-1975 to be shown as significant.

Over the period 1969-1975 (see Table 6.10), the average annual recruitment rate was 0.10 seedlings per established plant at each spring recording. Recruitment by seedlings was largely confined to the spring period, although in the period 1972-1975 more seedlings were recorded throughout the summer, probably because of the milder winters.

6.5.2 Recruitment of vegetative shoots.

Table 6.10 shows the rate of recruitment of new vegetative shoots into the population over the period 1973-1975 in each site. Analysis of the data indicates that there are no significant differences between sites or between years over the period 1973-1975. As expected, the majority of new rosettes are produced during the summer, although new rosettes are often recorded first at the spring record, i.e. they have been produced at some time between autumn and spring. This presumably reflects the time of recording in relation to the particular season. Over the whole period, 1969-1975, the average annual recruitment of vegetative shoots was 0.09 per established plant at the spring recording, almost exactly the same as the figure of 0.10 for seedlings over the same period.

Total recruitment per year over the period was thus about 0.20, compared to an annual mortality, including seedlings, of about 0.18.

Viola rupestris

Table 6.9

Annual recruitment of seedlings.

	Sites							
Year	2:2	2:3	3:2	3:4	6:2	9:2	9:3	Averages
1973	0.02	0.15	0.26	0.05	0.00	0.16	0.09	0.11
1974	0.10	0.00	0.00	0.05	0.00	0.09	0.04	0.03
1975	0.45	0.00	0.00	0.00	0.10	0.00	0.00	0.11
Averages	0.20	0.05	0.08	0.03	0.03	0.08	0.04	

The figures give numbers of seedlings per plant in the population at the spring recording.

Viola rupestris

Table 6.10

Annual recruitment of new vegetative shoots

Year	2:2	2:3	3:2	3:4	6:2	9:2	9:3	Totals
1973	0.07	0.00	0.00	0.05	0.00	0.08	0.04	0.03
1974	0.08	0.06	0.02	0.00	0.11	0.06	0.13	0.05
1975	0.04	0.08	0.15	0.27	0.19	0.00	0.00	0.01
Average	0.06	0.05	0.06	0.12	0.06	0.05	0.01	

6.6 Reproductive performance.

6.6.1 Age at first flowering and length of reproductive life.

Seedlings from the first two years of recording (1969 and 1970) were studied to estimate the length of time that they normally remained in the juvenile phase, and the proportion that died without flowering or persisted through the whole recording period without flowering.

Table 6.11 shows these figures, separated for each quadrat. It is clear that relatively few of these seedlings (10%) have flowered, but the indications are that plants normally flower first at 3-4 years old, although a few flowered first at 4-5 years, and one (10%) at 5-6 years. 67% of the seedlings died without flowering, and the remaining 23% were recorded for over 5 years without flowering. One seedling was recorded as flowering at 1-2 years old, although this may be a recording error, as growth is normally very slow in young Viola plants. Once the reproductive phase is reached, plants may flower continuously or discontinuously for a number of years. There is no indication that flowering increases mortality risk, and some individuals flowered 6 or 7 times during the period and were still alive at Autumn 1975.

6.6.2 Flower, fruit and seed production.

Viola rupestris produces two types of flowers; large open (chasmogamous) flowers, usually during a short period in May, followed by small closed (cleistogamous) flowers during the remainder of the growing season. The flowering percentages shown in Table 6.13 indicate the percentage number of plants producing either type of flower. Table 6.12 shows the numbers of each type of flower, and the number of fruits produced in each site in each year in the period 1972-1975. It is immediately obvious that flower production is greatly affected by where the plants are growing.

Viola rupestris

Table 6.11

Reproductive performance : Ages at first flowering, or length of time recorded without flowering, to Autumn 1975.

Age at first flowering * (Years)	Sites							
	2:2	2:3	3:2	3:4	6:2	9:2	9:3	Totals
0-1	0	0	0	0	0	0	0	0
1-2	0	1	0	0	0	0	0	1 (10%)
2-3	0	0	0	0	0	0	0	0
3-4	3	2	0	0	0	0	0	5 (50%)
4-5	3	0	0	0	0	0	0	3 (30%)
5-6	0	0	0	0	0	1	0	1 (10%)
6-7	0	0	0	0	0	0	0	0
Number dying without flowering	34	13	6	0	1	10	0	64
Number recorded over 5 yrs. from seed without flowering	8	7	0	0	2	4	1	22

* Using data from 1969 and 1970 seedling additions only.

Overall, 67% of these seedlings died without flowering, 23% were recorded for over 5 years without flowering, and 10% flowered.

Viola rupestris

Table 6.12

Annual flowering performance.

Parameter	Site							
	2:2	2:3	3:2	3:4	6:2	9:2	9:3	Totals
1973 data								
No. of cleistogamous flowers	20	13	2	1	1	32	3	72
No. of chasmogamous flowers	1	0	0	0	0	4	1	6
No. of ripe fruits	8	7	1	0	1	1 ch 21 cl	3	1 ch 41 cl
1974 data								
No. of cleistogamous flowers	24	5	2	1	2	35	10	79
No. of chasmogamous flowers	2	1	0	0	0	5	0	8
No. of ripe fruits	7	1 ch 1 cl	0	1	2	1 ch 9 cl	4	2 ch 24 cl
1975 data								
No. of cleistogamous flowers	16	3	1	0	0	48	4	72
No. of chasmogamous flowers	1	0	0	0	0	4	1	6
No. of ripe fruits	8	2	0	0	0	5	2	17
Total data								
No. of cleistogamous flowers	60	21	5	1	3	115	17	
No. of chasmogamous flowers	4	1	0	0	0	13	2	
No. of ripe fruits	23	1 ch 10 cl	1	1	3	2 ch 35 cl	9	

ch = chasmogamous
cl = cleistogamous

Fruits are from cleistogamous flowers unless stated otherwise.

Viola rupestris

Table 6.13

Flowering percentage.

Year	Site						
	2:2	2:3	3:2	3:4	6:2	9:2	9:3
1973	12	11	6	5	4	15	14
1974	16	9	2	5	9	19	17
1975	10	5	2	0	0	23	7
Averages	13	8	3	3	4	19	13

Analysis of the data presented in 6.12 indicates that there are no significant differences between years in flower or fruit production, but that there are differences between sites ($P < 0.001$) in flower and fruit production. Production of both types of flowers and fruits is higher in 9:2 and 2:2 than average ($P < 0.001$) and lower in 3:2, 3:4 and 6:2 than average ($P < 0.01$). Clearly, fruit and flower production is highest in 9:2 overall, followed by 2:2, and intermediate in 2:3 and 9:3. The variation in values for flowering relates clearly to vegetation form, as pointed out by Doody (1975) and Bradshaw and Doody (1978), and the significance of this is discussed below. The high loss of potential capsules from both types of flowers should be noted, and this loss is presumed to be by the removal of developing capsules by grazing sheep.

Doody (1975) and Bradshaw and Doody (1978) quote figures for seed production per 100 plants in each quadrat over the period 1969-1972. These are as follows:-

Site	No. of seeds/100 plants.
9:3 (most open)	133
9:2 (semiclosed)	86
2:2 and 2:3 (disturbed) data pooled	81
3:2 and 3:4 (closed)	0
6:2 (closed)	0

Table 6.14 shows the annual flower, fruit and seed production of Viola rupestris, expressed per 100 plants, or per capsule, as appropriate. As explained in 3.5.6., these are average figures and some are therefore subject to a degree of uncertainty. In general, these figures agree broadly with the conclusions reached by Bradshaw and Doody (1978), although a certain amount of seed has been produced in each of the three most closed sites since

1972, and site 9:2 ("semiclosed") had a higher production of seed over the period than site 9:3 ("most open"). As discussed in 6.5.1, and shown in Table 6.9, the differences in seedling recruitment between sites are not significant, although there are indications that seedling recruitment is higher in those sites where more seed is produced, except for site 9:3 where seedling recruitment is exceptionally poor.

6.7 Life cycle and reproductive strategy.

6.7.1 Species biology summary.

When a seedling of Viola rupestris germinates, usually in May, it first produces two large cotyledons, and usually a pair of true leaves within that year. Growth is slow, and the pre-reproductive phase is normally 3-5 years. Mortality of established plants is very low, with about 13% dying each year, and with individual plants persisting for long periods. Seedling mortality is higher, with about 25% of seedlings dying within their first year after germination. Mature individuals may flower repeatedly or intermittently over a long period, and there is no indication that flowering increases the risk of mortality. Flowers produced are of 2 types: 1. Open (chasmogamous) and 2. Closed (cleistogamous). Either is capable of producing fertile fruits, although many more fruits survive from cleistogamous flowers, partly because there are more flowers, and partly because the pedicel of the chasmogamous flower is longer, and thus the flower or developing fruit is more likely to be grazed. Mature fruits could be distinguished on morphological differences as originating from open or closed flowers.

Little is known of the pollination requirement or mechanism of the chasmogamous flowers. Insects have been observed visiting the flowers during the study period, and Doody (1975) records visits made by Bombus sp. and dipterans, although it is not certain whether cross- or self-pollination is the rule. Probably the details are similar to those given by Beattie (1969) for *Vv. riviniana*, *hirta* and *reichenbachiana*, although the severe conditions make insect cross-pollination less certain.

Dispersal of seed from ripe capsules is explosive, and seed may be thrown up to 3 metres by this mechanism of dehiscence (Bradshaw, pers. comm.). A small elaiosome is also present, and further dispersal may take place as a result of activity by ants, (Beattie and Lyons, 1975) as envisaged for *Polygala*. The length of life of *Viola* seed is unknown, although seeds stored in dry conditions have germinated after 4 years. Their longevity in the soil will doubtless depend on the soil conditions, but it seems likely that some amount of viable seed will build up in the soil and persist as a "seed bank". There is evidence that a prolonged chilling requirement is necessary, or a period of alternating cold and warm, and it proved very difficult to determine the optimum conditions in the laboratory. The true percentage viability of dispersed seed therefore remains unknown.

Established plants may also produce attached rosettes, which have been treated throughout this study as additional individuals, (following Doody, 1975) and they may themselves flower in their first or second year of production.

6.7.2 Life cycle.

Using data from all sites in all years, where available, it is possible to gain an insight into the average behaviour of this species on the Fell. Accordingly, a Life cycle has been constructed along the lines of that shown for *Polygala amarella*. This schematic representation is not intended to be representative of any one year or site, but is an indication of the behaviour of the species over longer periods. The considerable variation that

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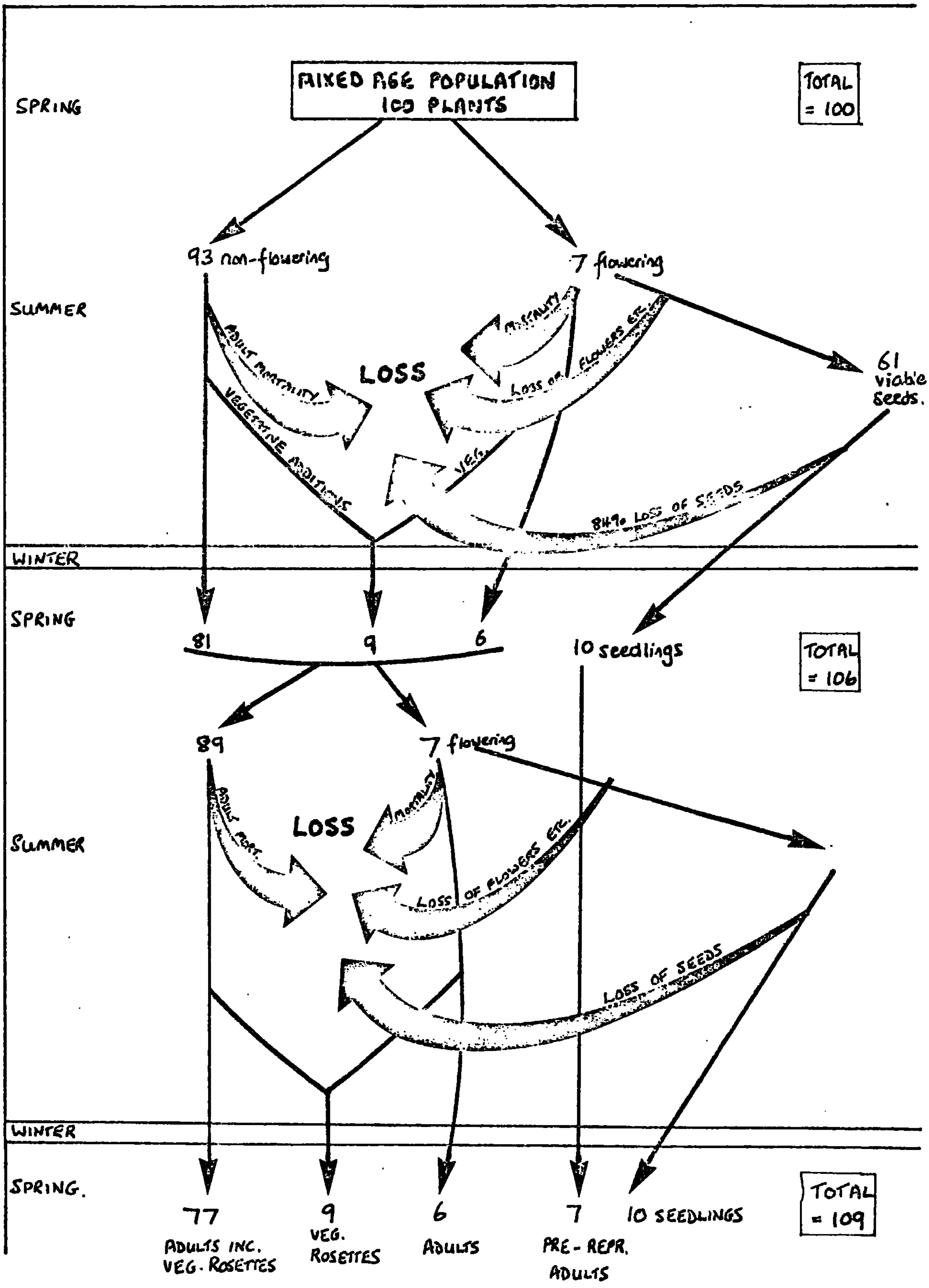
exists in reproductive performance between sites means that a simple average is not representative of either of the more extreme sites, although it approximates reasonably to the average behaviour of plants in intermediate sites.

The diagram is based on the following figures and assumptions:

1. An annual average mortality of 13% for non-seedling plants, based on records for 1969-1975.
2. Mortality of seedlings of 25% in their first year, based on records for spring seedlings over 1969-1975.
3. 7.5% of plants in the permanent plots produce flowers of either type per year (1972-1975 figures).
4. 61 seeds per 100 plants produced on average over the whole recording period, based on numbers of capsules known to have been produced in the permanent plots each year x the average number of seeds per capsule that year in collected capsules from adjacent sample plots.
5. An annual average loss of 65% of flowers before capsule dehiscence. Details of the processes involved are not known, but the majority are lost by grazing, and any proportion of unfertilised flowers is implicit.
6. Annual average recruitment (1969-1975) figures of 10 seedlings per 100 established plants, and 9 vegetative rosettes per 100 established plants have been calculated.
7. Emigration is assumed to equal immigration.
8. Seed viability is 100% amongst dispersed seed. This is unknown, but is, perhaps, the most reasonable estimate. It is recognised that seed may persist in the soil for a period of years, but this should not affect the numbers, unless these seven years were atypical, since this will be reflected in the number of seedlings recorded overall.

FIG. 6 4. LIFE-CYCLE DIAGRAM

VIOLA RUPESTRIS



9. The loss of unfertilised ovules is unknown.

A schematic life diagram showing 2 years in the life of a Viola rupestris population is presented in Fig. 6.4. The points of the life-cycle at which losses may occur, and where they are most significant can thus be seen, although they are not considered in detail as under Polygala because the plants in different sites have such different strategies. It is clear, though, that comparable losses occur at the seed⟶seedling and flower⟶fruit stage in all quadrats.

6.7.3 Life strategies with reference to plant environment.

It is clear that some of the observed differences between sites, particularly in reproductive performance and seedling establishment, relate to environmental differences. Bradshaw and Doody (1978) conclude, from data collected up to 1972, that Viola rupestris flowers more, survives longer, reaches a greater density, and produces more seed per plant in open sugar limestone situations than in closed vegetation. They suggest that "plants in the more or less open habitats exhibit the highest reproductive capacity and give the appearance today of growing in near-optimal conditions, whereas the survival of the plants in a closed sward is precarious". Table 6.14 compares most known parameters, derived as shown, for each of the sites. Success is difficult to assess. A population which has increased its numbers has been successful, but a population which has produced large amounts of seed that germinates elsewhere is also a success. Length of life alone can hardly be construed as success. Overall, therefore, it appears that plants growing in sites on sugar limestone turf on eroding edges, i.e. 2:3 and 9:2 are perhaps the most successful with a large increase in numbers and reasonably high establishment of seedlings, together with 2:2 on open disturbed turf away from an eroding edge. Plants

Viola rupestris

Table 6.14

Site comparisons

Site No.	Size (M^2)	Density M^{-2} at Aut.'75	Habitat/Vegetation Type	Half-life (yrs) of M-A pop.	Le (yrs)	% Flowering (1972/ 1975 only)	No. fruits per 100 plants	Av. seeds per 100 plants per yr. (1972/ 1975)	Seedling recruit. per yr. per 100 plants	Veg. recruit. per yr. per 100 plants	Change in nos. 1969/ 1975	Dist. cat. from TWM
2.2	1.2	79	Semi-open turf with open patches "Disturbed"	5.8	4.3	13	8.5	90	20	6	+53%	A
2.3	0.3	210	Open turf on eroding sugar limestone edge "Disturbed"	9.2	6.6	8	6.4	69	5	5	+66%	A
3.2	0.6	68	Closed turf	7.7	6.0	3	1.0	8	8	6	+29%	A
3.4	0.6	43	Closed turf	8.0	7.5	3	1.6	17	3	12	+30%	A
6.2	1.5	17	Closed turf	5.3	19.0*	4	5.3	42	3	6	-4%	B
9.2	0.6	220	Open turf on sugar limestone edge "semiclosed)	10.0	11.3	10	10.3	115	8	5	+33%	C
9.3	0.3	187	Open, flat and stony "Most open"	5.0	7.0*	6	5.9	66	4	6	-16%	C

Notes: DENSITY; Density of V. rupestris rosettes and shoots.

Le = LIFE EXPECTANCY, calculated for seedling additions. * Very small samples.

CHANGE IN NUMBERS: % increase or decrease in numbers of rosettes and shoots over the whole recording time.

DISTANCE CATEGORY: Distance from reservoir as explained in 3.1. A is closest to TWM.

in 2:2 have apparently greater recruitment, and the more stable and slightly deeper soil would probably favour this, but greater mortality and correspondingly shorter half-life. All these three sites showed increases in numbers of plants over the recording period, and the final densities of plants were high (2:2 had a lower density partly because the 4 metre quadrat included some less suitable ground). Site 9:3 is anomalous. Density of plants was very high, and flower and fruit production was good (Bradshaw and Doody found that it had the highest seed production over the period 1969-72), but length of life of plants appeared to be the lowest, recruitment was poor, and numbers declined over the period. The quadrat is very open and stony, although not on an eroding edge, and it may be a marginal habitat that is good under certain combinations of weather conditions, such as may have occurred in the recent past, but otherwise rather precarious. Vegetative recruitment was also low over the period, yet the high densities must have been reached in some way.

In the closed turf, densities of plants are generally much lower, and flowering performance is considerably worse. There are indications that plants in 2:3 and 9:2, the two eroding-edge sugar limestone turf sites, are the longest-lived, but plants within closed turf seem to be at least as long-lived as plants in 2:2 and 9:3. Bradshaw and Doody (1978) find that plants in eroding habitats have half-lives of 16 and 14 years, though these figures, with those of 8, 10 and 11 for closed habitats, are misleadingly high, and have been wrongly calculated. The corrected figures would be 6.8 and 5.8 for the two eroding habitats, and 4.0, 4.9 and 4.5 for the closed habitats. The differences are thus less marked, although confirmed by the half-lives shown in 6.14, which are calculated over a longer period. Recruitment from seed in the "closed" sites was slightly higher during the period 1972-1975 than previously recorded, although considerably lower than that in the eroding edge sites, but vegetative recruitment was as high or higher in the "closed" sites than elsewhere.

It is the combination of length of life (or mortality) and rate of recruitment that affects population numbers, and clearly those sites on eroding edges have an optimum performance in all respects, with the greatest possibilities for increase, reflected by the high densities present, and the increases made over the period. Vegetative recruitment, although it may be at a level as high or higher than seedling recruitment, is of less significance to the population. No new genetic recombinants are introduced, and fewer new "niches" are tapped, since a vegetative rosette, although capable of flowering, is dependent on the roots of its parent, and their combined reproductive performance should be lower than that of two separately-rooted plants. Further, a vegetative addition has a life no longer than that of its parent, and - unless the presence of extra rosettes increases the length of life of the parent plant - they must live for a shorter time than independent rosettes.

Plants from seed, in contrast, may arise from cross-pollination with its consequent greater variability, or from self-pollination where at least a degree of recombination may occur. Plants in closed habitats are therefore at a disadvantage in genetic terms as well as numerical terms compared to those in the optimum habitats. It is not clear whether the populations in the closed vegetation are remnants of a denser more vigorous population that existed when conditions were more open, or whether the _Viola_ persists in these marginal habitats anyway.

Valentine and Harvey (1961) in a review of the three localities known for _V. rupestris_ in Britain found that plants at Arnside, in open but fairly stable turf, with 30% bare ground, and only light rabbit grazing were very floriferous and produced abundant fertile seed, although densities were low. Plants at Long Fell (600M) were very small, growing in closed turf; they found that only 3% of plants produced capsules, while in the same year those at Arnside had numerous flowers and fruits, and those on Widdybank Fell flowered quite well. Plants from Arnside were found, in cultivation, to have few long shoots and a more lax growth compared to Widdybank plants. The observed densities and reproductive performance may thus be a combination of site factors, climate (where appropriate) and genetic differences.

Chapter Seven

Viola rupestris x riviniana.

7.1 Introduction.

The hybrid between the Common Violet Viola riviniana and the Teesdale Violet Viola rupestris occurs only on Widdybank Fell, as far as is known, within Europe. Small populations exist on the Fell, in habitats that are largely intermediate between those of its parents, and it is thus the rarest of the plants in this study. It flowers reasonably prolifically, producing flowers that are morphologically distinguishable from those of the parents, but as far as is known these are invariably sterile, and no seed is ever set. Reproduction, or more appropriately in this case, clonal growth (Harper 1977) is by means of new rosettes produced from root shoots (soboles), a character inherited from V. riviniana. Following Doody (1975), the unit of reproduction in the study is thus considered to be any rosette arising from a root shoot (or a seed).

There is little information on the biology of cross-pollination between the two parents, but presumably it occurs only very rarely, or the seed is very rarely viable, in view of the limited number of clones on Widdybank Fell, and its apparent absence from other sites where the two species grow together in Britain or elsewhere (Bradshaw, pers. comm.).

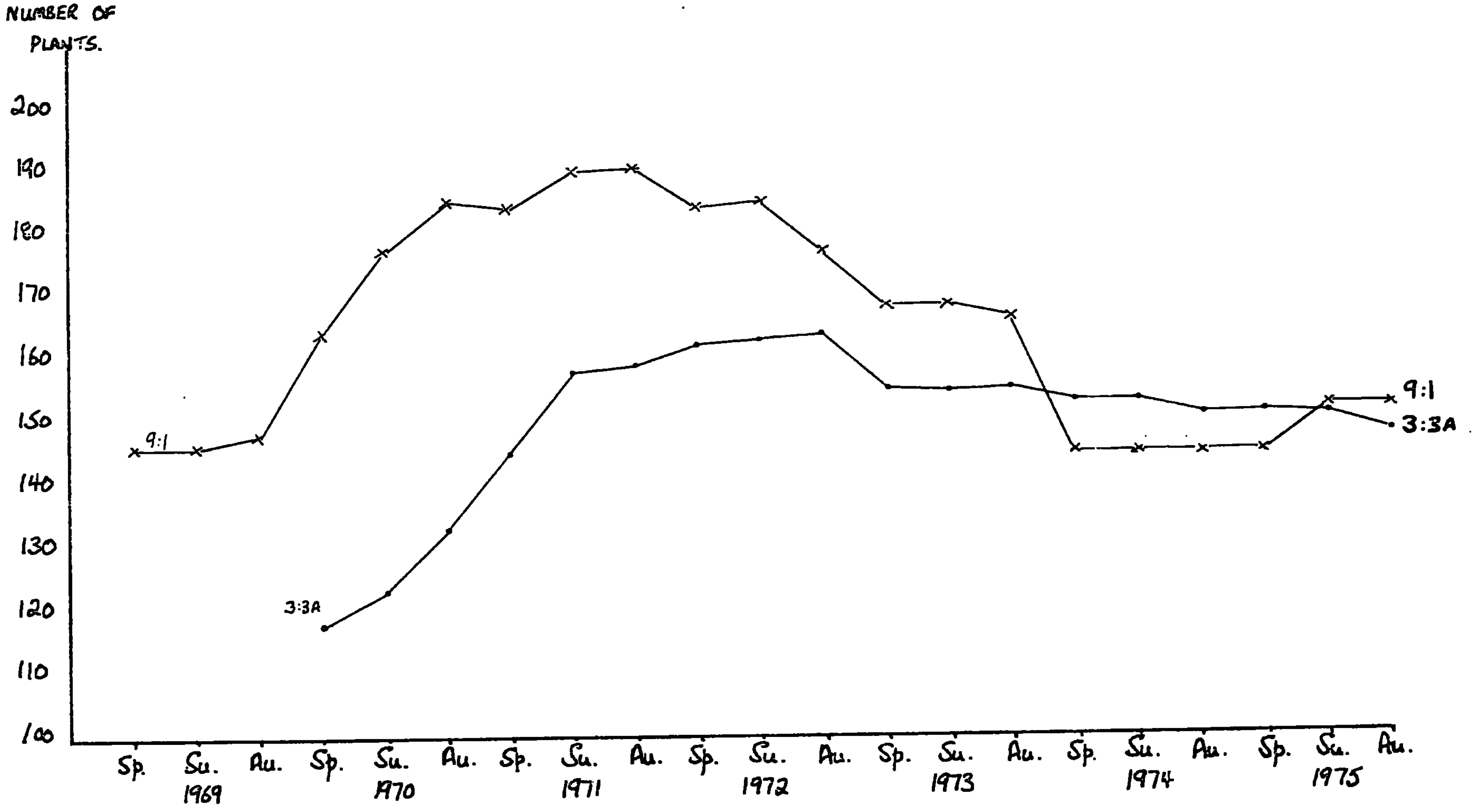
Individual rosettes within a clone are long-lived, and it is presumed that clones themselves are very long-lived, as they may be several metres across. At present, some 10 colonies are known on the Fell. (Bradshaw and Doody, 1978).

7.2 The recording sites.

Two sites were selected for recording this plant on Widdybank Fell, both in moderately stable, heavily-grazed turf over sugar limestone.

FIG. 7.1. VIOLA RUPESTRIS × RIVINIANA.

POPULATION FLUX, 1969 - 1975.



One site (3) was about 100 metres from TWM of the reservoir, and site 9 was over 500 metres from TWM.

Quadrat 3:3A lay on a south-west facing slope, near to V. rupestris sites 3:2 and 3:4. The vegetation was dense and completely closed, dominated by Festuca ovina, and Sesleria caerulea, with Plantago maritima, amongst other species.

Quadrat 9:1 lay between V. rupestris sites 9:2 and 9:3, although it lay in more closed stable turf than either of those. The vegetation was dominated by grazed Festuca ovina, and Sesleria caerulea, and the hybrid was very abundant in this small area.

Each permanent quadrat had a sample site, as explained, lying very close to it.

7.3 Population flux.

Table 7.1 shows the changes in numbers in the two permanent plots, together with the mortalities and additions that have resulted in these changes. Over the period Spring 1970-Autumn 1975 numbers of rosettes have remained exceptionally stable, with a slight increase (c. 6%) in numbers overall. Numbers were at their highest between Summer 1971 and Summer 1972, caused by unusually high recruitment of new rosettes in 1970-1971. Mortality was high in 1972, and numbers have remained constant since. In plot 3:3A, there was an overall increase of 30 plants (25%) during the period, whereas there was an overall decrease of 24 plants (16%) in 9:1 over the 6½ years. The lack of any great fluctuations probably reflects the low recruitment and high survival of the plants. The changes in numbers are shown graphically in Fig. 7.1.

7.4 Mortality rates and Life expectancies.

7.4.1 Age-specific mortality.

Table 7.2 compares mortality rates between different age-classes using all the plants of known age in the study sites. As previously discussed, the sample size decreases for the older age-classes.

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Table 7.1

Separate additions and mortalities in permanent plots, totalled.

Season	New shoots	Mortalities Date begins interval	Change in pop. nos. + or −. Date begins interval.	Pop. nos. including new adds.	Pop. without adds. until after 1st. winter
1970:					
Spring			+18	282	282
Summer	25	9	+18	300	275
Autumn	27	15	+11	318	268
1971:					
Spring	26	12	+19	329	303
Summer	31	7	+1	348	291
Autumn	8	15	-3	349	287
1972:					
Spring	12	13	+2	346	334
Summer	15	18	-7	348	321
Autumn	11	19	-18	341	305
1973:					
Spring	1	0	0	323	322
Summer	0	4	-2	323	322
Autumn	2	27	-23	321	318
1974:					
Spring	4	2	0	298	294
Summer	2	3	-2	298	292
Autumn	1	0	0	296	289
1975:					
Spring	0	7	+7	296	296
Summer	14	16	-3	303	289
Autumn	13			300	275

Viola rupestris x riviniana

Table 7.2

All plots, year class survival compared.

	Autumn figures Period of survival in years					
Year first recorded	0-1	1-2	2-3	3-4	4-5	5-6
1970	23 0.7391	17 .8235	14 1.0000	14 0.9286	13 0.8462	11
1971	41 0.8537	35 0.9429	33 .9394	31 .8710	27	
1972	58 .9655	56 .9821	55 .9091	50		
1973	30 .8667	26 .9615	25			
1974	3 1.0000	3				
Totals in each yr. class, less mixed-age pop.	155	137	127	95	40	11
Fraction surviving	$\frac{137}{155}$	$\frac{127}{134}$	$\frac{95}{102}$	$\frac{40}{45}$	$\frac{11}{13}$	
Proportion surviving	0.8839	.9478	.9314	.8889	.8462	
Mortality	0.1161	.0522	.0686	.1111	.1538	
Statistical significance from mean.	NS	NS	NS	NS	NS	

Analysis of the data indicates that no significant differences exist between age-classes, and mortality is therefore assumed to be age-independent, with an average annual mortality of 0.093, i.e. about 9% of plants die each year, on average.

It is reasonable, therefore, to calculate half-lives for the decay of age cohorts, or the depletion of the mixed-age population, in the expectation that these will give an adequate description of the behaviour of the population. Table 7.3 shows half-lives calculated for the mixed-age populations and cohorts of additions up to 1971 for each quadrat. The mixed-age population in 3:3A clearly survives better than that in 9:1, calculated over a slightly longer period, and there is considerable variation in the calculated half-lives of subsequent additions. The hybrid is, clearly, very long-lived, as expected from the low annual mortality rates, and the likely estimated turnover time for all the plants in a sample will be between 20 and 45 years, or possibly even longer if the plants added in 3:3A in 1971 are as long-lived as they appear to be. On the basis of an average annual mortality rate of 0.093, an average length of life for individuals of 10.25 years has been calculated.

7.4.2 Annual mortality.

Table 7.4(b) shows the annual loss of plants, expressed as mortality per plant at each autumn record, over the period 1969-1975 for each site. Inspection of the data indicates that mortality may be greater in site 9:1 than 3:3A. Analysis of the data, as described in 3.5.4 indicates that there are differences between years and between sites, ($P < 0.001$). Further analysis indicates that mortality in 1969-1970 is higher than expected ($P < 0.001$) and lower than expected in 1972-1973 ($P < 0.05$), and confirms the indication that mortality is higher in 9:1 than

Viola rupestris x riviniana

Table 7.3

Half-lives of mixed-age populations and age cohorts (in yrs)

Age Group	Site 3:3A	 9:1	 All quadrats
Mixed-age pop. Aut.'69-Aut.'75	NR	5.10	-
Mixed-age pop. Aut.'70-Aut.'75	11.60	-	6.93
Autumn 1969 additions	NR	7.88	-
Spring 1970 additions	NR	3.87	-
Summer 1970 additions	8.70	3.65	4.33
Autumn 1970 additions	8.70	5.33	6.93
Spring 1971 additions	23.10	9.90	13.90
Summer 1971 additions	23.10	5.78	9.90
Autumn 1971 additions	No deaths	8.66	9.90

All half-lives calculated up to Autumn 1975

3:3A ($P < 0.001$). Annual mortality of all plants is found to be approximately 0.10.

7.4.3 Seasonal mortality.

Table 7.4(a) shows the observed variation in mortality between seasons for each quadrat. Analysis of the data indicated that survival in the period between spring and summer (April/May-July) was lower than expected ($P < 0.05$) while that in winter and autumn was no different from average. This contrasts with the findings of Doody (1975) that mortality appeared to be greater in the summer 6 months (although the difference was not significant). Clearly the timing of the recording in relation to the growing season may be critical, especially if mortality is concentrated over quite a short period in the early growing season, although the findings that mortality is at its lowest between May and July suggest that mortality would have to be particularly high very early in the growing season, tailing off rapidly, if it really is related to the growth period. Further records over the critical period would be necessary to resolve the difference, which may be a recording artefact, or may be a genuine difference between years.

7.5 Recruitment.

Recruitment, as described in 7:1, is entirely by the production of new rosettes on root shoots from existing plants, except for the seed which originally gave rise to the clone. No seedlings were observed during the period of the study, and it is likely that they are extremely rare. Recruitment over the whole period of study was, on average, 0.124 rosettes per plant per year. Table 7.5 shows the annual rate of recruitment per established plant over the period 1969-1975 for each site. Although recruitment is higher on average in 9:1, the data are too heterogeneous

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Table 7.4

Seasonal and annual mortality

(a) Seasonal mortality.

Season	Site 3:3A	 9:1	 Averages
Autumn 1972		0.06	0.06
Spring 1973	0.05		
Summer 1973	0.00	0.00	0.00
Autumn 1973	0.01	0.01	0.01
Spring 1974	0.01	0.15	0.08
Summer 1974	0.01	0.00	0.01
Autumn 1974	0.02	0.00	0.01
Spring 1975	0.00	0.00	0.00
Summer 1975	0.01	0.03	0.02
Autumn 1975	0.03	0.07	0.05
Site Averages	0.02	0.04	0.03

(b) Annual mortality.

Year			
Aut. 1969-1970	NR	0.20	0.20 (1 site)
Aut. 1970-1971	0.05	0.15	0.11
Aut. 1971-1972	0.11	0.14	0.13
Aut. 1972-1973	0.07	0.07	0.07
Aut. 1973-1974	0.05	0.15	0.10
Aut. 1974-1975	0.05	0.11	0.08
Site Averages	0.05	0.14	0.10

Viola rupestris x riviniana

Table 7.5

Annual recruitment of vegetative additions

	Quadrat		
Year	3pp 3A	9ppl	Averages
1969	NR	17/146 0.116	17/146 0.116
1970	18/118 0.153	66/132 0.500	84/250 0.336
1971	32/130 0.246	33/173 0.191	65/303 0.215
1972	23/153 0.150	15/181 0.083	38/334 0.114
1973	2/155 0.012	1/167 0.006	3/322 0.009
1974	3/153 0.020	4/141 0.028	7/294 0.024
1975	4/151 0.026	23/145 0.159	27/296 0.091
Averages	82/860 0.095	159/1085 0.147	241/1945 0.124

Figures expressed as number of additions per adult plant in the population at the spring recording.

for analysis to indicate any difference either between sites or between years. 1970 and 1971 have much greater recruitment rates than other years, although the differences are not significant, and obviously much of the recruitment was in 9:1 only.

7.6 Reproductive performance.

As mentioned in 7.1, this hybrid Viola is completely sterile, as far as is known. Its flowering performance is not therefore considered in detail here, as it apparently plays no part in the regulation of the population numbers. No evidence was found that plants were more likely to die after flowering. Doody (1975) records that both open and closed flowers are produced, in a similar fashion to the two parents, but that relatively more open flowers compared to closed flowers are produced than either parent.

7.7 Life cycle and reproductive strategy.

7.7.1 Species biology summary.

The hybrid Violet is a long-lived perennial (Average length of life 10.25 years; estimated population turnover time 20-45 yrs.) which has no true method of reproduction. It spreads and persists by a form of clonal growth in which new rosettes are produced from soboles (root shoots) in a similar manner to V. riviniana. The rosettes die back to the rootstock over the winter period. On average, 0.124 new rosettes are produced per plant per year, and 0.09-0.10 plants per plant in the population die each year. Thus, a slight increase in numbers was observed over the recording period, but the inherent rate of increase is very low, and the longevity is an essential feature of the plant's persistence.

7.7.2 Strategy.

A clone of Viola rupestris x riviniana derives from a fertile seed produced by a chance cross-fertilisation of the two parents. No hybrids are known anywhere in Europe except on Widdybank Fell, where only a few clones are established, and no new clones have been observed to arise since the distribution of plants on Widdybank Fell has been known (Bradshaw, pers. comm.). It may therefore be assumed that the production and establishment of such seed is an extremely rare event. Thus it is critical for clones to have a high rate of survival. No information is available for the age of the established clones, although pattern analysis (Kershaw, 1957) might give some indication of this. Within the clones, the length of life of individual rosettes is reasonably long, as explained, and a low recruitment of individuals is required to maintain the population. In the short-term, the method is clearly quite successful, as numbers in the permanent quadrats have increased slightly during the recording period. However, the extreme rarity of the hybrid in a vegetation type that has been broadly similar for up to 3000 years, and where both parents have probably been present, indicates that severe constraints are operating in the long term. This restricted distribution may be simply a facet of the recent origin of the hybrid, perhaps caused by very unusual conditions at some period in the past; alternatively, the evidence may suggest that the hybrid is severely limited as to the habitat it can colonise, or clonal life-span is restricted.

Chapter eight

Mortality patterns.

8.1 Age-specific mortality.

Over the past 20 years, a considerable amount of data has been collected on the mortality rates of known-age perennial plants. One of the most striking features of these data is that mortality of non-seedling plants has been shown to be almost invariably independent of age, (e.g. Harper 1967). In other words, death is a function merely of numbers, and such factors as the size of a plant, the length of time it has been established, or the size of its root system, do not, apparently, assist survival. *A priori*, it might be expected that increasing degree of establishment, at least up to an age where inherent mortality pressures (i.e. old-age!) began to operate more strongly, would increase the likelihood of survival. In the longest published studies on perennial plants, Tamm (1972, 1972a) presents the results of studies on various orchids, and *Primula veris* over periods up to 27 years. No other comparable data are available over this time scale, and his findings are thus critical for an attempt at understanding the relationship between age and mortality of long-lived individuals. For *Primula veris* in three separate quadrats, he found that individuals in Site I showed virtually no mortality at all for eight years, but then declined relatively rapidly for the next eighteen years; individuals in Site II died in considerable numbers over 3 years, remained constant over 5 years, and then died off at a faster rate; and individuals in Site III died off at a more or less constant rate throughout the whole 26 year period (calculated half life, 50 years). Tamm relates the pattern of mortality in sites I and II to changing environmental conditions, and it is tempting to regard the individuals in the most stable site,

Site III, as best representing the decay rate of populations of _Primula veris_. In studies of such long-lived individuals, it is more or less impossible to separate the effect of changing environmental conditions from the effects of age-dependent mortality as it would occur in more stable conditions. The observation, however, that a population of _P. veris_ does exhibit age-independent mortality in stable conditions over such a long period, indicates that this species probably follows the commonly-observed pattern as long as conditions do not change, and that there is no intrinsic effect of age on likelihood of mortality.

Dactylorchis sambucina in a dry meadow exhibited more or less age-independent mortality over a 27 year period, although plants of the same species in a 'mesic' wooded meadow showed a sudden increase in mortality after 12 years, which Tamm again relates to changing environmental conditions, associated with a decline in the total numbers of the plant. Perhaps the most striking behaviour is exhibited by _Listera ovata_ which has a very low, constant rate of mortality over the whole 28 year period.

In summary, therefore, Tamm's observations suggest that it is likely that a range of perennial herbs, growing in varied grassland conditions will exhibit age-independent mortality over an extremely long period if conditions remain stable, and there is no indication at all that individuals of great age survive better than young ones.

There is evidence that certain types of grasses, particularly tussock-forming ones exhibit very different survivorship or depletion curves, as discussed in Chapter 1, and these are not considered further here. There is a very small amount of evidence that indicates that decay of other plants, excluding grasses, may not fit the pattern of negative exponential decay. Hett (1971) and Hett and Loucks (1971) observed the survival of a cohort of seedlings originally studied by Curtis (1959) of Sugar Maple, <u>Acer saccharum</u>. There was a gap in the data from 1956-1965, although careful selection was made to ensure that later results would be comparable. They considered that the survival of the seedlings best fitted the power function model, although they found little real difference between its correspondence with that or with the negative exponential curve. The power function curve indicates that increasing age increases the chances of survival i.e. mortality rate decreases with increasing age. There are few examples published where decay rates are related to both the negative exponential and power function curves, although Hawthorn and Cavers (1976) compared their data for the survival of <u>Plantago spp</u> cohorts, and found that it fitted the negative exponential curve better. Such studies that fit observed data to mathematical models may seem abstract, but if the observed data correlate closely with models, then predictions may be made on that basis, as is done with populations that fit the negative exponential by predicting the half-life and total turnover time, for instance.

The species studied for this thesis have now been under observation (up to Autumn 1975) for 6-7 years, longer than the half-life for many of the species, and long enough to gain an idea of the mortality patterns of each species. In general, mortality has been shown to approximate to negative exponential. A negative exponential curve may be defined by the equation:-

$$y = y_0 e^{-bx}$$

where y is the number of individuals at time t, y_0 is the initial population number, x is the age in years, and b is the mortality constant. Thus decay is solely a function of numbers. Transformation of numbers onto a log scale produces a straight line which indicates the decay rate. This corresponds to the Type II decay envisaged by Pearl and Miner (1935) and later Deevey (1947), although considered at that time to rarely occur in nature (i.e. in the animal world - little was known about plant mortality at that time). A power function curve, in contrast, assumes a decreasing risk of mortality through life, and is defined most simply as: $y = y_0 x^{-b}$

where transformation to a straight line may be made by taking the $\log_e$ of both sides to give:-

$$\mathrm{Log}_e y = \log_e y_0 - b \log_e x$$

where b is the mortality constant.

This curve has some of the characteristics of Deevey's (1947) Type III curve, though it need not be so extreme, and is more likely to lie midway between II and III.

Gentiana verna shows decay approximating to age-independent mortality, except that there is an indication (not significant) that 2-3 year olds are more likely to die, amongst those known-age individuals followed, than earlier or later age-classes. This is probably accounted for by the findings that Gentiana is more likely to flower at 2-3 years old, and is somewhat more likely to die after flowering; the effect would not be expected to be great in view of the low percentage of Gentiana plants that flower.

Polygala amarella shows mortality that does not depart significantly from age-independence, except that plants were found to be more likely to survive at 3-4 years, and that this difference is significant. No convincing reason can be adduced for this, and it is not clear whether it is really a significant time in the life-cycle or not. Nevertheless, it is simply a single-year difference superimposed on a general pattern of age-independent decay, and there is no indication of greater correlation with the power function model, or other model decay curve.

Viola rupestris x riviniana shows no indication at all of age-dependent mortality. Although the figures for mortality between year-classes are variable, there is no sign of a general trend towards increasing or decreasing mortality with age. The hybrid is a long-lived perennial with few resources being put into flower production, and none into fruit production, and it might be expected that no particular age could be singled out as that where mortality would be most likely.

Mortality figures for *Primula farinosa* are available for a 9 year period, but unfortunately only for a very small sample of plants. The decay of the mixed-age population and of subsequent additions, lumped, are shown below in Table 8.1.

Table 8.1

Age-specific mortality in Primula farinosa plants. Widdybank.

a. Mixed-age population. Autumn figures.

Year	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
No. at risk	25	23	22	22	20	20	17	16	13	11
No. dying		2	1	0	2	0	3	1	3	2
Mort.		0.08	0.04	0.00	0.09	0.00	0.15	0.06	0.19	0.15

Table 8.1 (Cont'd.)

b. Known-age plants.

Age-class	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9
No. at risk	15	11	11	10	9	5	3	2	1
No. dying	4	0	1	1	2	2	1	1	
Mortality	0.27	0.00	0.09	0.10	0.29	0.40	0.33	0.50	

No significant differences could be detected between year-classes, partly because of the small samples involved. The general indications are that mortality is age-independent, with slight indications of increased mortality amongst older age-groups. These correspond to the extremely dry period of 1975-1976, and it is not possible to disentangle the effects of year and age where so few cohorts have been followed.

For a small population studied at Cassop, in lowland Durham over the period 1973-1976, the values for the mortality rate of the mixed-age population are:

1973-74	1974-75	1975-76
0.12	0.16	0.28

These samples were also very small, and again the apparent trend to increasing mortality with age coincides with the 1975-76 drought, and few conclusions can be drawn.

The only real evidence of departure from age-independence amongst the species studied is observed for Viola rupestris. The figures for decay of known-age plants of V. rupestris are shown in Tables 6.1, 6.2 and 6.3, and their level of significance discussed in section 6.4. These figures suggest that there is a decreasing rate of mortality with increasing age. The data for an imaginary cohort based on the survival rates shown in Table 6.2 have been transformed by plotting on a $\log_e - \log_e$ scale in Fig. 8.1. The indications are that Viola rupestris plants decline at a rate corresponding to a power function curve, where the calculated value of b is 0.4087, i.e. their decline may be characterised as:

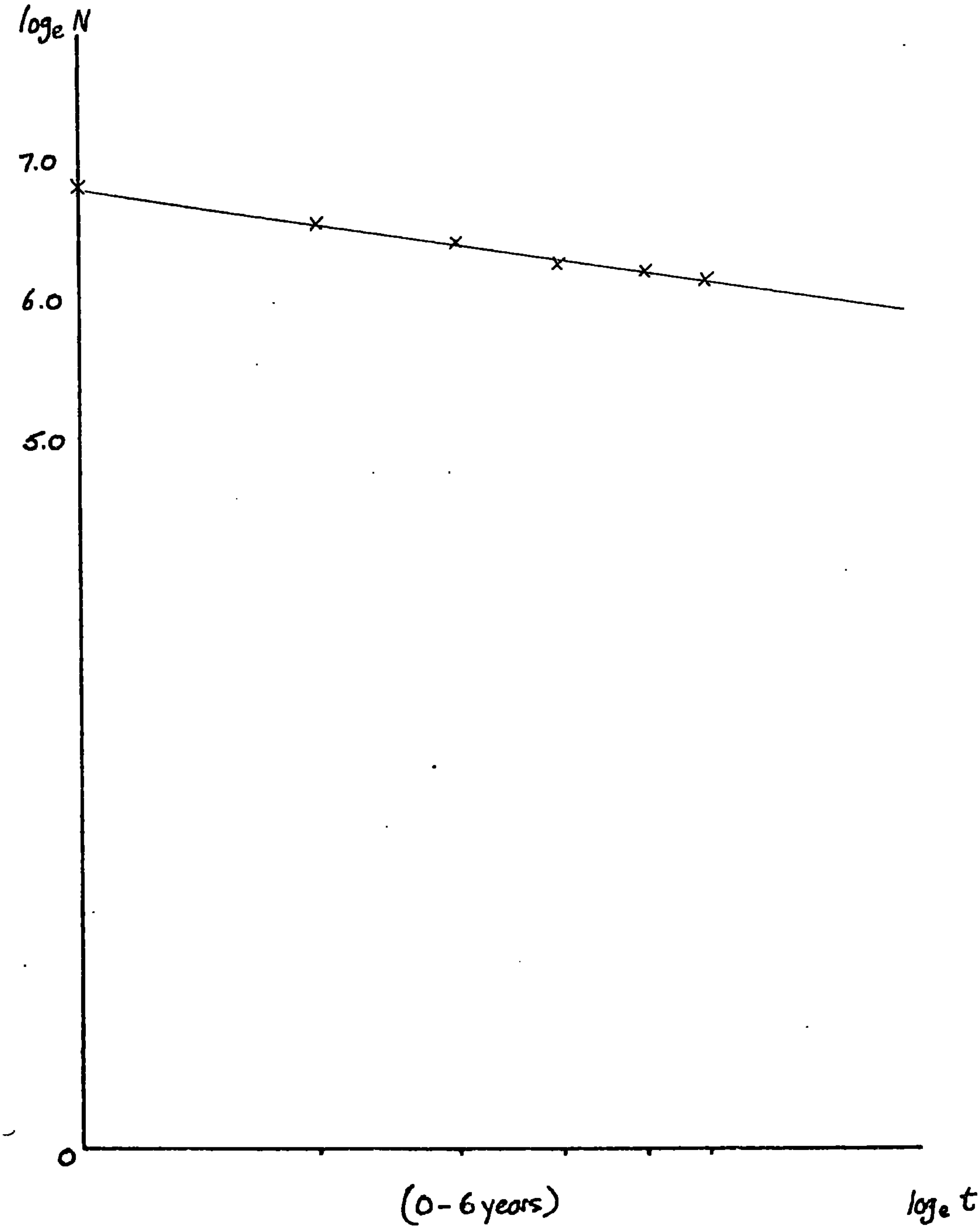
$$y = y_0 x^{-0.4087}$$

The data are not a perfect fit, and more samples would be required to test the validity of this generalisation; however the indications are that decline of known-age individuals in Viola rupestris does not follow a negative exponential curve, but may follow a power function curve.

Age-independent mortality implies that the mortality factors operating on the population act more or less equally on plants of all ages. If it is assumed that a plant becomes more established during its life e.g. expands its root system, and enlarges its above-ground parts or capacity for producing them each year, then it might be expected that older individuals would survive better, unless this increasing establishment caused some mortality factor other than resource depletion to act more severely (e.g. larger plants might be more likely to be grazed). It would be expected, a priori, that an established plant would compete better than newly-established plants in closed vegetation, so either increasing age does not bring about any change in degree of establishment (possibly because competition is too great, although this is difficult to visualise for V. rupestris in open situations), or the plant's susceptibility to others decreases with increasing age. It is probable that age-specific mortality is a function of habitat and plant growth form, and further work may show that there are more examples of plants with

FIG. 8.1 VIOLA RUPESTRIS

DECAY OF KNOWN-AGE PLANTS, POOLED DATA.



other than age-independent mortality outside the perennial herb in grassland situation.

8.2 Annual and seasonal mortality.

Throughout the results section (Chapters 4-7), there have been frequent indications that species behave differently, to some extent, in different years. In some respects, the degree of difference has been surprisingly small, particularly with regard to mortality, where significant differences are the exception, although some variation may be obscured because plants in different sites have reacted quite differently to a given set of annual conditions, making it considerably more difficult to generalise about the behaviour of a species with regard to different annual conditions.

Meteorological data are available for Widdybank Fell over the period of this study, and - since management conditions in the sites have remained reasonably constant, - it is tentatively assumed that weather in some way or another is the most likely factor behind the observed changes. There are, however, considerable difficulties involved in relating the type of parameters presented in this study to changing weather conditions, and it is normally impossible to make definite statistically-acceptable correlations of observed performance with particular climatic variables. Firstly, problems lie in the interaction of all the different weather factors at different times, and the considerable effects of the weather in one or more previous years, as discussed briefly in 3.5.2b. Secondly, the fact that different sites react differently to given weather conditions may indicate, in part, that the microclimatic conditions are different in each site, and that the Meteorological station data is by no means necessarily a good indicator of the conditions around the plants.

Arnold and Monteith (1974) showed that there was quite a close correlation between 'mean screen temperature' at the Widdybank Meteorological station and the ground level mean temperature in a grass tussock in an exclosure on Widdybank Fell. However, this is unlikely to apply in all situations (e.g. frost hollows), and other weather variables measured at screen level may be less closely related to ground conditions, as is well-known.

Thirdly, internal population factors such as age-structure, or density of plants (and density of the surrounding vegetation) may interact with, or override weather effects.

Clearly, extreme weather conditions may have such an obvious effect on the performance of the plants that correlation is inescapable, and there is evidence that the drought of 1976 had such an effect on the mortality rate of plants in this study (Fordham, pers. comm.). Over the period 1968-1975, the most significant observed annual differences in mortality were as shown below:-

Aut.1968-Aut.1969	Mortality significantly higher than expected in Gentiana verna.
Aut.1969-Aut.1970	Mortality significantly higher than expected in all species studied.
Aut.1970-Aut.1971	Mortality lower than expected in Polygala amarella.
Aut.1971-Aut.1972	Mortality higher than expected in P. amarella.
Aut.1972-Aut.1973	Mortality significantly lower than expected in all species except V. rupestris, (in which it was low, but not significantly so).

It is immediately obvious, therefore, that conditions in 1969-1970 were sufficiently unusual as to bring about increased mortality in all the species studied, and that conditions in 1972-1973 were sufficiently unusual as to cause increased survival in three out of four species.

Various authors have attempted to correlate mortality or particular changes in population numbers with climate, although often these take the form of observations of major changes after catastrophic events (e.g. Ehrlich et al. 1972). Newman (1965) found that rosette senescence in the winter annual Teesdalia nudicaulis was considerably hastened by prolonged drought, although this was much less marked in Aira praecox growing under similar circumstances (Newman, 1967). Wilson (1959) found that exposed plants or parts of plants were likely to die of drought in the spring, especially during sunny weather in the conditions prevailing in the Cairngorms, and that snow cover prevented this. Wells (1967) found no evidence that even extremes of climate affected the survival of Spiranthes spiralis, while Bradshaw and Doody (1978) conclude that mortality of Viola rupestris is increased by colder winters, according to the following table:-

Year	Feb. mean air temp.	Survival rate April-Oct.
1969	-3.5°C	0.82
1970	-2.0°C	0.88
1971	2.2°C	0.94
1972	0.5°C	0.95

although expectation of such a clear correlation is likely to be optimistic. Some authors have related high mortality to particular periods of the year, and this may give an insight into the primary mortality factors operating. Sarukhan and Harper (1973) found that mortality in three Ranunculus spp is highest when the survivors are making their maximum growth, or just before. Hawthorn and Cavers (1976) found that mortality is highest in the period when active growth starts for two

Plantago spp., and again in late summer, but is very low in the extremely cold winters. Sagar (1959) found that the main period of mortality in *Plantago lanceolata* is in May-June. Thus, in general for perennial herbs in grassland, it seems likely that the main mortality stress is caused by competition for resources, or other factors operating strongly in the early growing season, and that this may be influenced by particular weather conditions at or before this time. Clearly, such events as severe frosts well after growth has started will be likely causes of mortality, and the different phenology and strategy of different species will give them different relative advantages according to the conditions. The findings of the present study are that mortality is higher during the winter months, although this contrasts to some extent with the suggestion of Doody (1975) that mortality tended to be higher, in these species, in the summer months, although not clearly higher. The weather during the period of this study (1972-1975) was distinctly different from that of the period studied by Doody (1968-1972) with a tendency to milder winters, but late cold springs in the latter period, although the differences may have been due to slightly different recording times, which were themselves a response to the late springs.

In an attempt to appreciate the possible causes of the very different mortalities in the periods Autumn 1969-Autumn 1970 and Autumn 1972-Autumn 1973, the mortalities were first separated into the three recording periods to see which periods were particularly unusual. During the high mortality year 1969-1970, mortality amongst the four species was high or average in the winter period; during the spring-summer it was high or average; and during the summer-autumn it was average or low. Therefore, the increased mortality shown in all four species over this period occurred in winter and spring. During the low mortality year 1972-1973, mortality was average or low over the winter, low or very low from spring-summer, and low or average from summer to autumn. Thus survival was apparently favoured throughout the whole year, but particularly during spring compared to usual years.

Table 8.1 shows selected weather measurements for the two years 1969-1970, and 1972-1973 compared, where available, to the averaged values for the recording period 1968-1975. Examination of the data for possible differences indicates that 1969-1970 (high mortality) had the following characteristics:-

1. A much wetter than average winter (Nov. - Apr.).
2. A much drier than average May.
3. A colder than average winter.
4. A warmer than average May and June.

1972-1973 (low mortality) had the following characteristics:-

1. Drier than average from Jan - March, but wetter than average through April and May.
2. A very dry June.
3. A rather mild winter, though colder than average in April. Less cold than 1969-1970 in all winter months.

Sunshine or windspeed were not greatly different over the relevant period, according to monthly mean figures.

Figs. 8.2 and 8.3 show the weekly average values for rainfall, sunshine, maximum air temperature, and grass minimum temperature over the growing periods in 1970 and 1973. It is obvious that 1973 was as cold through this period (mid-March to end June) as 1970, and, in fact, suffered more from heavy frosts in April and late May. So, presumably spring and late frosts are not a major mortality factor. Air temperature rose rather

Table 8.1

Weather measurements for Widdybank Fell Meteorological Station, Grid ref. NY 818289, alt. 510M. Monthly average figures.

	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	
1969-70	58	290	170	203	340	92	164	41	60	112	142	163	Rainfall (MM)
1972-73	36	295	168	91	72	50	165	92	7	111	173	78	
Ave. 1968-75	107	186	148	190	140	141	108	86	89	93	108	127	
1969-70	7.0	-1.7	-2.5	-2.7	-4.9	-3.6	-1.0	4.6	6.8	7.6	6.7	7.5	Mean min. air temp. (°C)
1972-73	3.9	-1.6	-0.4	-0.7	-1.8	-1.1	-0.5	3.6	7.3	10.9	7.6	6.7	
Ave. 1968-75	4.3	0.1	-0.7	-1.2	-2.8	-1.7	0.1	2.9	5.8	8.4	8.6	6.5	
1969-70	9.9	0.7	0.0	-0.4	-2.0	-0.4	2.1	8.8	11.9	10.6	12.7	10.7	Mean air temp. (°C) $\left(\frac{T_{max} + T_{min}}{2}\right)$
1972-73	7.0	2.6	2.5	1.3	0.9	2.7	2.7	7.2	11.1	12.1	11.7	9.9	
Ave. 1968-75	7.2	2.6	1.8	1.2	-0.2	1.3	3.8	7.0	10.1	12.0	12.4	9.7	
1969-70	3.8	-3.2	-4.4	-4.5	-5.2	-4.9	-3.3	1.7	2.7	6.6	6.2	7.5	Mean Grass min. (°C)
1972-73	1.3	-1.2	-2.0	-2.7	-3.0	-3.7	-2.7	1.7	5.2	6.0	5.6	5.3	
1969-70	-	6.5	4.5	5.5	7.3	6.2	5.9	5.0	4.0	6.4	4.2	6.0	Wind speed (M/sec.)
1972-73	4.5	6.5	5.4	5.6	7.4	5.2	4.6	4.1	5.1	3.9	4.9	4.4	
Ave. 1968-75	5.9	6.8	7.2	7.5	5.6	5.5	4.9	4.8	4.6	4.7	4.3	5.1	

FIG. 8.2. WIDDYBANK FELL WEATHER

MEAN AIR MAX. TEMPERATURE AND GRASS MIN. AS WEEKLY AVERAGES.

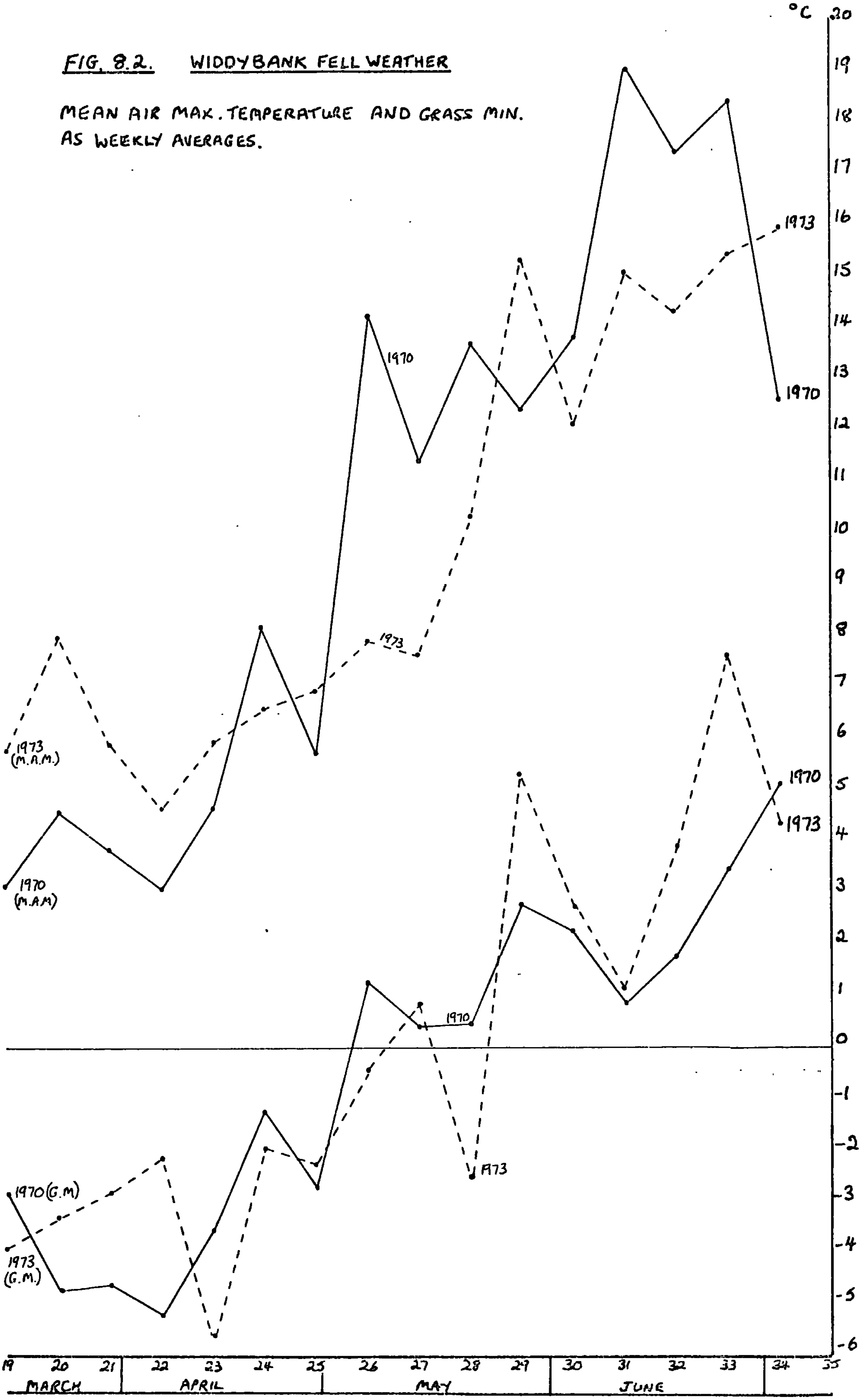
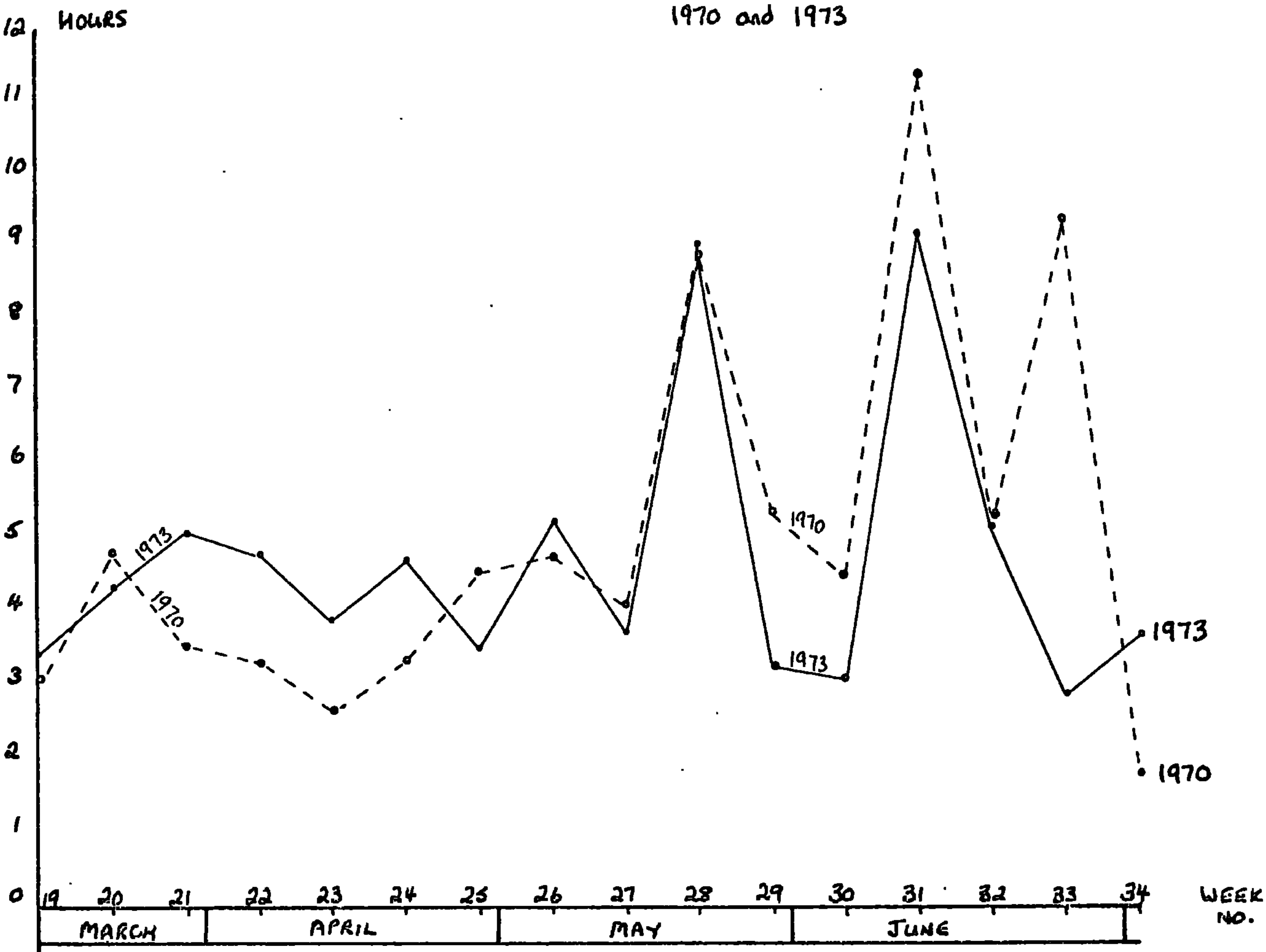
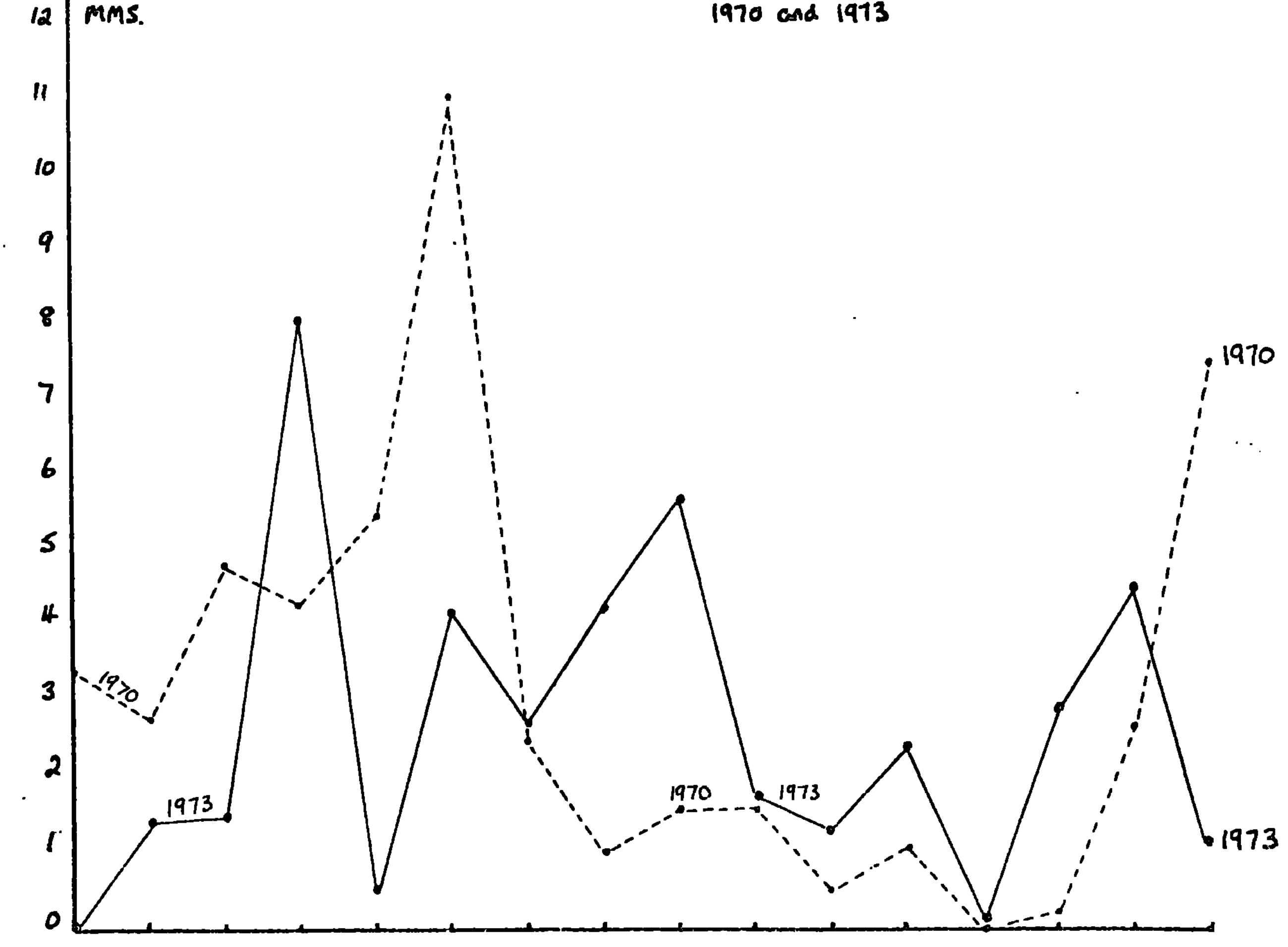


FIG. 8.3, WIDDYBANK FELL WEATHER,

a. WEEKLY SUNSHINE AS DAILY MEANS (HOURS)
1970 and 1973



b. WEEKLY RAINFALL AS DAILY MEANS (MM)
1970 and 1973



more steadily in 1973, after an early warm period in March, although the difference from 1970 is not likely to be great. The highest air temperatures were reached in 1970 (19°C in week 31) at a time of very low rainfall, but 1973 was quite warm and dry at this period, and there is no evidence that June was the peak mortality period in 1970. Perhaps the most significant factor is that May was dry, sunny and warm in 1970, compared to 1973. Welch and Rawes (1969) have shown the very high drainage rate and frequency of drying out of the sugar limestone soils, and it is probable that the effects of the wet winter in 1969-70 will have been rapidly lost on the freer-draining soils. Thus, dry, sunny conditions, coupled with low incidence of ground frosts and more wind than average at the time when plants are beginning to grow fast, and many are flowering, is quite likely to have promoted increased mortality by desiccation and competition for resources. Further, initial recording for most species was carried out some time during May, such that the mortality - if May was the critical month - would be split between "winter" and "spring" as shown.

Generalising from the available data, it seems likely that moderate frosts in the early growing season are not a major cause of mortality. The period of highest mortality of the whole study period included a wet, cold winter, followed by a dry, warm, sunny, windy May. It is not possible to separate the effects of each factor, although it seems most likely, from other evidence, that the frost and wet during the non-growing season will have had relatively little effect, and that the main factors will have operated during the early growing season. The major causes of mortality are presumed to be desiccation or resource depletion caused by warm, frost-free conditions in May at a time of water shortage aggravated by sun and wind.

8.3 Cohort mortality.

Several authors have observed that cohorts of plants born in different years have quite different decay rates (e.g. Antonovics, 1972; Williams, 1970; and Williams and Roe, 1975), and Harper (1977) has summarised these observations and pointed out how puzzling it is that survivorship of some cohorts for some species should apparently be determined at the time of recruitment. It is obvious from the results of this study that cohorts of all species born in different years have different decay rates and corresponding half-lives, sometimes strikingly so. For example, half-lives of different cohorts of Gentiana verna in one quadrat vary from 6.30 years to 0.39 years, while cohorts of seedlings of Polygala amarella in one quadrat vary from 3.47 to 11.95 years. There is no evidence that a given year affects all cohorts in all sites similarly e.g. that all cohorts 'born' in 1972 were longer-lived than those 'born' in 1973; the variation is apparently random. Since it is as apparent in the clonal growth pattern of Gentiana verna and the Viola hybrid as it is in the seedling recruitment of Polygala and Viola rupestris, it is unlikely to be a genetic effect. It may, therefore, be caused by conditions in the plants' first year affecting the rest of their life; i.e. by whether they get off to a 'good' or 'bad' start in life; or it may be due to purely random variation particularly where small samples are involved; or, thirdly, it may occur because a cohort born in year a is subjected to different conditions at each stage of its life to one born in year a+1 or a-1, and although such generations quickly begin to overlap, some difference in mortality is likely to result overall.

Chapter Nine

Reproductive strategies and adaptation

Since Harper (1967) gave his pioneering Presidential Address to the British Ecological Society entitled "A Darwinian approach to plant ecology", there has been a considerable quickening of interest in the different ways in which plant populations may maintain themselves in their particular environment, and how different strategies of life have evolved in response to the pressures of the environment. The general accumulation of observations on the dynamics of plant populations has already been discussed in general terms, but alongside this there has developed a branch of ecology concerned specifically with the life strategies of plants. Cole (1954) in a classic paper on the population consequences of natural history phenomena drew attention to the critical factor of timing of reproductive events in the life cycle, and consideration of the features that affect the potential rate of population growth. In 1967, MacArthur and Wilson crystallised current ideas of adaptive strategy into the "r and k" theory, in which two types of organisms were proposed: k-selected organisms tend to have long lives, and the proportion of energy and other resources devoted to reproduction is small. In contrast, r-selected types have a short life expectancy and a relatively large reproductive effect. In these contexts, r refers to the maximal rate of natural increase, and k refers to the carrying capacity of the habitat. Pianka (1970) refined the idea, which originally related particularly to island species, and pointed out that most species lay along the theoretical r-k continuum. The r endpoint of the continuum represents the ecological vacuum where there are no density effects and no competition, and the optimum strategy is to put all possible resources into producing as many offspring as possible. At the k extreme, most effort is put into maintenance and minimal replacement by a few fit offspring. Over a long period of time, r for a stable population = 0, and thus Smith (1954) pointed out that environmental resistance must exactly balance biotic potential at that point, and therefore $\underline{r}_{max.}$ is an indicator of the environmental resistance. The concept is too theoretical, and depends on too many factors to be a readily useable one, but it is an important idea and is useful when comparing the strategies of similar plants. Although it may appear simplistic to categorise all plants according to two evolutionary pressures and in many ways it is an over-simplification, the concept has proved to be of considerable value in encouraging consideration of the pressures on plant life-cycles, and the different ways in which plants may react to different environments. Gadgil and Solbrig (1972) stress that the concept is only meaningful on a comparative basis, for which there are no absolute criteria. Their work with biotypes of Dandelion in natural situations (Gadgil and Solbrig, 1972; Solbrig and Simpson, 1974) has shown that a particular biotype characterised by higher output of smaller seeds, higher proportion of biomass devoted to reproduction, and lower competitive ability is dominant in disturbed habitats over a biotype with typical k-selected attributes. The latter biotype was also found to become dominant in the stable conditions of the experimental situation. In later experimental work (Solbrig and Simpson, 1977) they found that perturbation of experimental plots considerably affected the final equilibrium of biotypes, and that - as predicted - one biotype (type D) dominated the undisturbed plots, and another (type A) dominated the disturbed plots. Moore (1976) quotes Sterk (1975) who showed that populations of Anthyllis vulneraria behaved differently in unstable open coastal conditions compared to populations in more stable inland sites in Holland. Plants on the coast produced more flowers per plant, began flowering earlier, and mortality was related to stresses in the abiotic environment (e.g. drought). In contrast, plants in the more stable, closed inland situations had fewer flowers produced by older plants, and mortality was considered to be the outcome of competitive interplay.

The broad concept of r- and k- induced adaptation is thus supported by experimental and observed evidence, although much of the accumulated evidence is circumstantial.

Hickman (1975) studied Polygonum cascadense in a mountain environment apparently rather similar to that of Upper Teesdale, where erosion constantly produced a mosaic of stable, unstable and intermediate habitats. He found that plants of the Polygonum allocated proportionately more resources to reproduction in harsh open habitats than in the more moderate habitats, and that these differences were "environmentally-cued" rather than genetically-determined. He states that such environmentally-cued adaptive behaviour is unique among plants studied, and he relates it to the short-term unpredictability of the habitat.

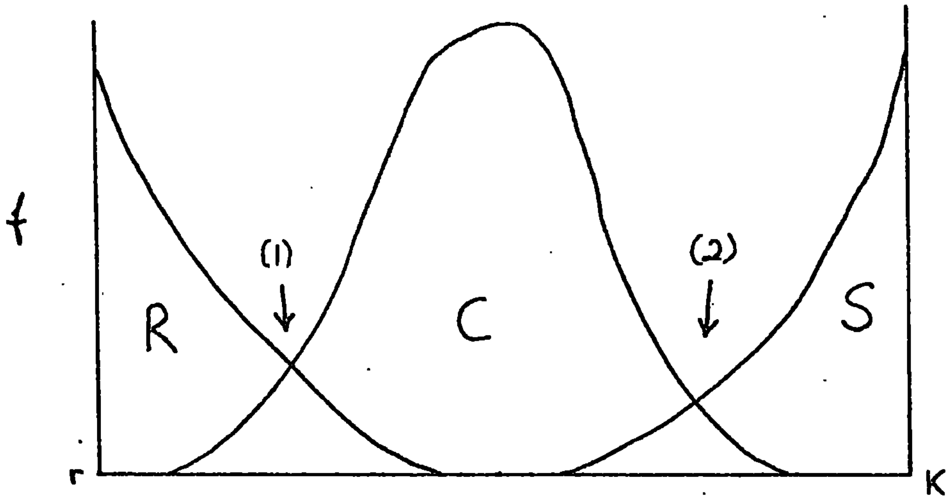
Grime (1977) has developed and refined the r and k hypothesis further. He concludes that there are 2 main external factors limiting plant biomass: 1. Stress, which acts to restrict production, e.g. shortages of light, water, nutrients, etc.,

2. Disturbance: partial or total destruction of the plant biomass by such activities as herbivores, pathogens, man, wind damage, soil erosion, etc.

As a result of the conclusions of Milne (1961) that the word "competition" was rarely defined, and despite the suggestion by Harper (1971) that it be abandoned through misuse, Grime (1973) defines competition as "The tendency of neighboring (sic) plants to utilise the same quantum of light, ion of mineral nutrient, molecule of water, or volume of space". A degree of intimacy is clearly implied. He goes on to distinguish three fundamentally different forms of natural selection that have taken place during evolution. These are:

1. C - selection for highly competitive ability, depending on the ability of the plant to maximize growth in productive undisturbed conditions.
2. S - selection, causing reductions in reproductive and vegetative vigour allowing endurance of continuously unproductive conditions arising from environmental stress, or severe resource depletion by the vegetation.
3. R - selection, associated with short life span and high seed production evolved in severely disturbed but potentially productive conditions.

Although similar to the <u>r</u>- and <u>k</u>- theory, it differs in that stress-tolerance is recognised as a distinct strategy evolved in intrinsically unproductive habitats or where there is extreme resource depletion by the vegetation itself. Grime suggests that there are 2 critical points along the <u>r-k</u> continuum: (1) where intensity of disturbance becomes insufficient to prevent exclusion of ruderals by competitors, and (2) where the level of supply of resources is depleted below the levels required to sustain the growth rates of competitors, and selection begins to favour the more conservative physiologies of the stress-tolerators. Grime (1977) illustrates it as follows:-



He recognises, however, that the basic scheme is both incomplete and misleading in that the simple linear arrangement of the strategies does not provide for the wide range of equilibria which may exist between stress, disturbance and competition which has provided conditions for the evolution of various types of secondary strategy. Grime (1977) recognises four such secondary strategies, and it is these that seem to be particularly applicable to many of the Teesdale plants. They are:

(1) C-R. Adapted to low impact of stress, and competition is restricted by moderate intensity of disturbance (e.g. fertile cattle pastures and meadows).

(2) C-S. Stress-tolerant competitors, adapted to undisturbed conditions experiencing moderate intensities of stress (e.g. open forest, scrub on infertile soils).

(3) S-R. Stress-tolerant ruderals, adapted to lightly disturbed unproductive habitats (e.g. droughted rock outcrops, crevices in cliffs and walls).

(4) C-S-R plants. Confined to habitats in which competition is restricted to moderate intensities by the combined effects of stress and disturbance, (e.g. unfertilised pastures and meadows).

It is found that the R-strategists are a reasonably homogeneous group, while the C-strategists have a wide range from perennial herbs to trees, and S-strategists have the widest range, from lichens to trees.

The general features of stress tolerance are: slow rates of growth, evergreen habit, long-lived, low phenotypic plasticity, shy flowering and the presence of mechanisms that allow the vegetative plant to take advantage of temporarily favourable conditions (e.g. the presence of functional leaves throughout the year). Low palatability is also suggested a priori on the grounds that the slow growth rate would cause slow recovery from defoliation These theories have been elaborated fully because the population characteristics of the species studied are now known in reasonable detail in a series of habitats in one of the most unusual areas, botanically and environmentally, in Britain. Their strategies, particularly in view of their known or presumed survival from the last glaciation, are thus of particular interest in the light of current theories.

The hybrid Violet, V. rupestris x riviniana, has perhaps the simplest, but in some ways the most revealing, life strategy. Its rate of increase is necessarily limited to one component only, that of clonal growth giving rise to new rosettes that become independently rooted. A proportion of resources (Harper and Ogden, 1970) is, nevertheless, devoted to flowering, and Bradshaw and Doody (1978) record that the hybrid produces as many flowers as V. riviniana and more than V. rupestris. Doody (1975) with confirmation from the results of this study, found that flowering was consistently higher at site 9 than at 3, and over the whole recording period, up to 1975, there was a higher production of flowers at 9 in every year. Further, mortality was found to be considerably and significantly higher at 9 than at 3. Site 9 is apparently more disturbed, by inherent soil instability than 3, with somewhat more open vegetation, and it is much more apparent that it is over sugar limestone. In other words, plants in the more disturbed site devote more resources to flower production and live less long than plants in more closed turf, closely fitting the general tenets of r-k or R-C-S adaptive pressures. Yet, there can be no adaptive significance in this for the hybrid. The devotion of more resources to flowering cannot result in increased seed production or increased seedling recruitment. Further, selection can only have taken place at the original establishment stage, since the established clone can make no real genetic adaptation. Therefore, unless it is merely chance that clones with quite different characters became established in those habitats most suited to them, or if some selection happened to operate amongst hybrid seedlings to favour that plant which would have the best-adapted characters when adult, then it must be presumed that these apparent adaptive differences are in fact "environmentally-cued", as shown by Hickman (1975) for Polygonum cascadense. Further experimental work is clearly required to test this possibility before conclusions can be firmly drawn, but it is obvious that the behaviour of this hybrid is of general interest to the discussion of adaptive strategies. Vegetative recruitment in the hybrid was not significantly different between the sites, and was maintained generally at a low level, slightly higher than necessary to balance mortality. There is no information on loss of rosettes before they appear in the quadrat (i.e. before they are first recorded), but it is presumed that this is low or non-existent. The overall strategy is therefore an exceptionally cautious one, where about 90% of the population is maintained each year, and each plant produces, on average, a new vegetative addition every eight years (or one in eight plants produce a new addition per year) for which the post-emergence survival rate is as good as an adult's. A proportion of resources is wasted in the production of open and closed sterile flowers at as high, or higher rate than that of the parents. Although there is evidence that the more floriferous clone (at 9) has higher mortality, there was no particular difference in density of plants between the two sites, and it seems likely that the clone in the more disturbed site (9) also has a greater rate of vegetative recruitment (supported by the figures over the whole period, which show higher recruitment in 9:1 although not significantly so). Presumably the more open and disturbed nature of site 9 allows established plants to produce more rosettes under the less competitive conditions prevailing, despite diversion of more resources to flowering.

Gentiana verna has an essentially similar strategy to that of the Viola hybrid, although the generation time is considerably shorter and the factors behind the reliance on vegetative reproduction are different. Gentiana verna has two potential methods of increase, or two values of $\underline{r}$; vegetative reproduction by the production of new, independently-rooted rosettes, and the production of seed. In the study area, the gentian behaves as a short-lived normally polycarpic perennial; in the study sites, no gentians produced capsules because of severe grazing by sheep, and it may be that the species would act as a monocarpic perennial if capsules were allowed to develop. As far as the permanent study plots were concerned, $\underline{r}_{seed}$ was more or less zero with only 3 seedlings recorded in the period of study altogether, and it is probable that the strategy of this species has adapted or adjusted in response to this pressure, which has existed over a long period. Normally, about 7% of plants in the quadrats produce flowers; virtually all of the resources diverted to this are wasted under the present conditions, and it is argued in 5.7 that this diversion of resources to flower production is likely to be decreasing. In its potential, Gentiana verna lies between the extremes of *r* and *k* , but it is likely that *k*-selection is operating to push it away from *r*- and reduce its intrinsic rate of increase. The gentian differs from the hybrid Violet in its strategy in that its rate of turnover and replacement is considerably faster, but also in the fact that the population consists of a much greater number of clones, and that addition of variability from seed (which is very mobile) set elsewhere, in less grazed conditions, is likely to be a constant factor. It is very similar in that it relies on the production of relatively few new plants (0.32 per plant per yr.) into which a considerable proportion of resource is placed, but whose survival rate is very high (like V. rupestris x riviniana, there is no information on the loss of Gentiana ramets before they emerge, but it is presumed to be low). Both waste a proportion of their resources by producing flowers (in 3-7% of individuals on average, per year) that do not or cannot develop fruit. It is of interest that, despite their comparable strategies, the gentian is the commonest plant amongst those studied within the area, while the Viola hybrid is the rarest (and one of the rarest plants in Britain). The hybrid is confined to a very specific habitat, as described, while the gentian occurs in a wide range of closely related habitats.

One of the parents of the Viola hybrid, V. rupestris, has quite a different strategy. It is a long-lived perennial polycarpic plant, capable of repeated-producing over a long period of time without apparent detriment to the plant, and its strategy is the most complex of those observed. From a purely numerical point of view, *r* has two components; those of seed production and vegetative rosette production. Seeds may be produced from potentially (though not necessarily regularly) outbreeding chasmogamous flowers, or from inbreeding cleistogamous flowers. Seed from cleistogamous flowers constitutes a high proportion of the total production, but no distinction is made between seed and seedlings from each type once the seed is dispersed (for practical reasons!), and it is assumed that survival of each type is equivalent, although this may not be the case in certain habitats. V. rupestris reaches reproductive maturity at 3-5 years old, and once this state has been reached, it may flower repeatedly for a considerable number of years, a few plants having been recorded as flowering seven times. No doubt they can continue to flower until death. On average, over the period 1972-1975, 7.5% of plants produced flowers of one or both types per year, but because of the repeated production of most flowering individuals, the percentage of plants recruited that actually produce flowers at some time must be considerably lower, since it is only necessary to replace those flowering individuals that die to maintain the average percentage. The seeds produced are reasonably heavy (1.20mg., from Bradshaw and Doody, 1978) and are produced at the average rate of 61 seeds per 100 plants per year which must be considered low amongst grassland plants (cf. 100 per plant for Thesium humifusum, 270 per plant for Polygala calcarea, or 98,000 per plant for Orobanche elatior growing in chalk grassland (Salisbury, 1975), or up to 3 million from one plant of Juncus effusus (Salisbury, 1976), although these figures are not directly comparable as they are per flowering plant, rather than per plant in the population). 16% of this seed appears to survive to produce seedlings (see Fig. 6.4 and section 6.7.2), of which 75% survive their first year. This seems to be a fairly moderate policy, midway between the high seed survival of Vulpia membranacea, for instance, where 90% of seeds germinated, (Watkinson, 1975) through the more comparable figures of 21% and 6% survival for Sedum smallii and Minuartia uniflora respectively (Sharitz and McCormick, 1973) and the other extreme shown by orchids, broomrapes, etc., where only a few seeds from hundreds of thousands survive (Salisbury, 1942).

The second means of increase is by a form of vegetative reproduction, as described in 6.1, in which new rosettes are produced on stem shoots from the parent plant. The significance of this has been discussed in 6.7.3 with reference to the population's survival. This vegetative reproduction is estimated to occur at about 9 new rosettes per 100 plants per year, and - although the rosettes are thought to always remain attached to the parent - a degree of advantage is attained in terms of increased space, incoming light etc. utilised, although it cannot really be regarded as reproduction any more than above-ground branching. The true recruitment rate of the population is provided by the number of seedlings, and, from a strategic point of view, the vegetative branching must be regarded as a way in which established plants can increase their degree of cover in the vegetation.

Particular interest attaches to the different behaviour or strategies of Viola rupestris populations under different environmental conditions. The general features of this have been discussed under section 6.7.3, and are discussed here only as they may relate to life strategies and their adaptive significance. In closed turf (plots 3:2, 3:4 and 6:2), plants have a shorter life, much reduced flowering and lower production of seeds, and there is some indication that they may have a longer pre-reproductive life (see Table 6.11, but the sample of plants followed through from birth is manifestly inadequate), and they occur at a lower density when compared to plants in open, semi-open or disturbed situations. In one "closed" plot, vegetative recruitment is well-above average, though not in the other two. The vegetative growth is not, however, a true reflection of an increased ability to survive, for reasons explained. It would thus appear that the Viola rupestris plants are ill-adapted to the closed situations as no characteristics have developed that fit the population for such situations. A reduced ability to reproduce would demand an increased capacity for self-maintenance (i.e. increased longevity) for the population to remain stable. It is probable that this lack of adaptation relates to the Teesdale environment which is "a constantly varying complex, unstable in detailed pattern, but stable in overall make-up"., (Bellamy et al. 1969). Thus, Viola rupestris grows optimally in open disturbed habitats, where most seedlings establish, the plants flower better, produce more fruit and live longer. In some areas, this habitat will have changed away from the optimum, by colonisation and stabilisation, and the Violets will have found themselves in increasing competition with other species. This results in a decreased reproductive performance, initially environmentally-induced only, and a decreased length of life through increased stress. This would be the first step towards the evolution of a k-selected biotype with increased powers of self-maintenance, but the process will go no further if there are insufficient long-lived individuals to survive and reproduce in the changed habitat, and the species will be ousted from the closed grassland. It is postulated that the populations in closed grassland are declining, and will continue to do so unless a more k-adapted biotype establishes, or the habitat maintains or increases its level of disturbance such that V. rupestris can survive without adaptation.

In addition to the observed differences in behaviour, the theory is borne out by the absence of the Violet from most of the apparently similar grassland on the Fell, and that the predominance of an inbreeding mechanism would be likely to slow the rate of adaptation to any change. It would be unwise to base too much on only 7 years of recording and observation, and experimental work would be necessary to test much of the truth of these statements, although the suggestions correlate well with the observed facts. The adaptive strategy, or lack of adaptability in V. rupestris clearly relates to its reproductive process. Clausen (1962), for instance, has shown that populations of Viola often undergo subdivision, and that character divergence occurs between local colonies of single species, whether reproduction is by means of cleistogamous flowers only, or not. As Grant (1971) and Williams (1975) have pointed out, uniparental reproduction by cleistogamy gives rise to offspring that are very similar to the parent, and differs little from vegetative reproduction in this respect. Although we know the approximate proportion of seeds produced by cleistogamous or chasmogamous flowers for the V. rupestris population, we do not know the proportion of chasmogamous flowers that are self-pollinated, and the proportion of "uniparental" seed may be higher than it appears. Beattie (1976) has shown the presence of buffered gene flow in chasmogamous flowers, and he argues that cleistogamy is the optimal mode of reproduction for Viola colonies. Clearly, though, a degree of recombination is required for adaptation to environmental changes, and the ability of a population to respond depends to a large extent on the frequency of crossing within the population, and with plants from other populations. It would be interesting to know the frequency of cross-pollination within the V. rupestris populations in Teesdale; this may be very low in view of the relative scarcity of pollinators and low production of chasmogamous capsules, and this may relate to its observed inadaptability.

Polygala amarella reproduces solely by seed. In Teesdale, it acts as a rather short-lived perennial, with the capacity for repeated-production. It reaches reproductive maturity at 2-4 years old usually, and may then be polycarpic, with some plants having flowered for five years. Only a small percentage of individuals 'born' actually produce flowers during their lives. The annual percentage flowering is about 16% of plants, but rather less individuals produce flowers during their lives. Relatively few large seeds are produced, at the rate of 9 per flowering plant, although the capacity is considerably higher and is restricted by factors such as grazing. On average 88% of these seeds appear to be lost, but after germination, survival of seedlings is as high as that of adult plants.

As indicated in Section 4.7.4., there are observed differences in the general strategy of plants in different sites on Widdybank Fell. Plants at Site 6 live longer, have a lower flowering percentage, and - hardly surprisingly - have a lower recruitment than plants in other Widdybank sites. They exhibit the typical k-adapted strategy of reduced effort put into reproduction and more into self-maintenance, although there is no further evidence to show whether this is genetic or environmental. As discussed in 4.4. , the observed environmental site differences between 6 and some other sites are small, and it may be that plants at 6 have become adapted to closed turf because they have survived such conditions for longer than plants at site 7 which is closer to open eroding edges. P. amarella is a habitual inbreeder, and as

Grant (1971) and Williams (1975) have pointed out uniparental sexual reproduction gives rise to offspring very similar to the parents, and differs little from vegetative reproduction in this respect. In other words, plants at 6 may have adapted better to closed turf conditions than plants in similar situations at site 7, possibly through longer exposure to such conditions, or possibly through the presence of more suitable genes initially, combined with genetic isolation from adjacent colonies.

One general point of interest concerns Harper and White's (1974) suggestion that early mortality amongst seedlings represents the shedding of the ill-adapted "genetic load" of the species, caused by normal recombination. They suggested that the specific risk period should thus be lower or absent in apomicts, although no information was available on the survivorship of such species. It may be of interest, in this context, that, whilst the seedlings of P. amarella and V. rupestris are quite similar in size and general morphology, those of the totally-inbreeding P. amarella survive considerably better than those of the partially outbreeding V. rupestris. It would be of considerable interest to compare the survival of seedlings of V. rupestris from seeds from cleistogamous flowers with those from chasmogamous flowers known to have been cross-pollinated, since many other factors may be acting in the comparison between species.

Finally, Primula farinosa was studied in two widely different situations, in Teesdale and in a site in lowland County Durham. Few data are available, but it is apparent that the species has rather different strategies in the two situations. Primula farinos is a reasonably long-lived perennial, which can produce large numbers of small seeds when capsules are allowed to develop. The sole true method of increase is by seed, although secondary rosettes may develop on the parent, and are able to flower although they do not become independently-rooted. Plants are able to flower repeatedly through their life, producing 4-8 flowers in an umbel, although in Widdybank these only rarely developed into ripe capsules due to removal by grazing sheep. In Cassop, seed was usually produced, and the average number of seeds per inflorescence over the period 1973-1975 was 418±62, although a proportion frequently suffered from fungal attack.

Table 9.1 shows the half-lives of mixed-age populations and subsequent additions of <u>Primula farinosa</u> populations on Widdybank and at Cassop. It is obvious that plants on Widdybank Fell usually live longer, with a half-life about twice that of the Cassop populations. Table 9.2 shows the rate of recruitment of new seedlings per plant in the different sites. Again, it is obvious that the populations behave differently, with recruitment at Cassop about ten times as high (over the period 1973-1975) as that on Widdybank.

The site at Cassop lay amongst damp <u>Sesleria</u> grassland as described in Chapter 3, with light grazing and trampling by stock or horses. The dampness and steepness of the slope meant that trampling had considerable effect, and hoof-marks were readily visible as areas of displaced turf. The site is essentially considerably more favourable than Widdybank Fell, with better climate and greater productivity, but much less stable. In this more productive but unstable site, <u>P. farinosa</u> appears to have a much faster turnover, greater fecundity, and better establishment of seedlings, although longer periods of observation on larger samples are required to verify this.

Although the species studied all have different strategies,

Primula farinosa

Table 9.1

Half-lives of mixed age populations and age cohorts (in years).

		Sites			
		Cassop pp 1	Cassop pp 2	Cassop Both	Widdybank 6:1
Mixed age population		3.85	2.48	3.59	7.70
Seedlings:	Spring 1969				8.50
	Spring 1970				4.50
	Spring 1974	4.33	NR		NR
	Summer 1974	2.25	NR		NR
	Autumn 1974	1.26	NR		NR
	Summer 1975	NR	1.25		NR

Primula farinosa

Table 9.2

Annual recruitment of seedlings.

	Sites			
	Widdybank 6:1	Cassop 1	Cassop 2	Cassop Ave.
1969	0.09			
1970	0.07			
1971	0.00			
1972	0.00			
1973	0.00	0.03	0.00	0.03
1974	0.06	0.09	0.20	0.10
1975	0.00	0.43	0.60	0.44
Site Averages	0.03	0.19	0.20	0.19

and have adjusted to the Teesdale conditions in different ways, the differences are relatively minor compared to the total range of reproductive strategies occurring amongst plants. The environment of the sugar limestone is a harsh one, where stress, competition and disturbance all play a part, and this combination of factors has probably prevented the successful survival of plants with widely differing strategies.

Chapter Ten

Environmental factors and conservation

10.1 Introduction.

The relevance of population dynamics studies, and in particular these Teesdale studies, to conservation has been thoroughly discussed by Bradshaw and Doody (1978 and in press). The species chapters in this thesis contain sections which outline the weak-points of the species' life-cycles and their susceptibility to management changes, and the effects of weather and adaptation to the environment have been discussed in Chapters eight and nine. This chapter considers further two factors which may be of considerable significance to the survival of the rare plants, in the light of the results from this study.

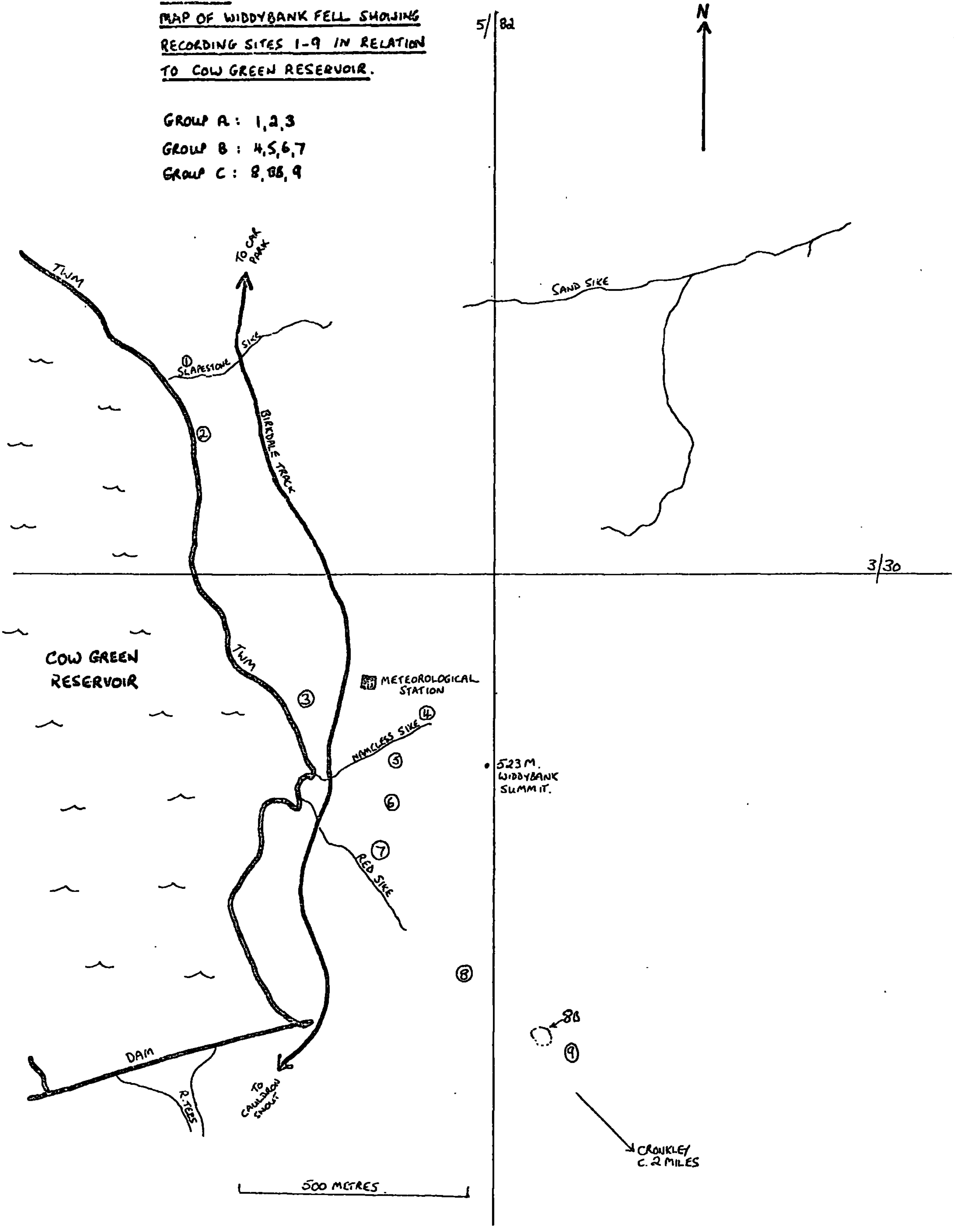
10.2 The effect of the Cow Green Reservoir.

The proposal, in 1965, to build a reservoir at Cow Green which would flood a considerable acreage of rare plant communities met with a great deal of resistance from scientists and many other interested parties (Smith, 1975). However, the reservoir construction proceeded despite the vigorous opposition, and some 21 acres of rare plant communities were flooded. Although the greater proportion of these communities remained, there were widespread fears that the presence of the reservoir might continue to affect the survival of the rare species by causing changes in the climate and watertable of Widdybank Fell, and - as described in Chapter three - the sites for this study were set up to monitor the effects of any such changes. Other factors have come into prominence, since the completion of the reservoir, which appear to be more likely to affect the unique plant-life. These include a huge increase in visitors to Cow Green, reaching an estimated figure of over 70,000 in 1977 (T.J. Bines, pers. comm.), and considerable erosion of the sugar limestone adjacent to the reservoir at an alarming rate (I. Findlay, pers. comm.). Investigation of these factors was not made part of this study, and, since other investigations on their effects are proceeding, they are not discussed further here, although their importance is considerable.

There is some evidence that the reservoir has slightly altered the climate by reducing the severity and intensity of frosts to a small extent (I. Findlay, pers. comm.), but a much longer period of recording will be required before this can be confirmed. Using the changes in numbers of plants over the whole recording period as the most reasonable general indicator of the possible effects of the reservoir, an idea of the effects may be gained by comparing the changes at distances A, B and C from the reservoir, where A is closest to the reservoir. On this basis, there is no clear trend for Gentiana verna; Viola rupestris increased strongly at all four A sites, decreased at the B site, and decreased in one out of two C sites. The Viola hybrid increased at the A site, but decreased at the C site, while Polygala increased at B, but decreased at all C sites to a greater or lesser extent. The initial impression, therefore, is that the plants closer to the reservoir are doing slightly better than those further away, although no firm conclusions can be drawn, for several reasons. Firstly, there are considerable variations in site factors overlaying, and probably dominating, the effect of distance from TWM. Secondly, it is not necessarily true that the effects of the reservoir - if any - on climate will simply decrease linearly with distance from the reservoir. Changes in rainfall, for instance, might be most marked on the first slopes

FIG. 10.1.
MAP OF WIDDYBANK FELL SHOWING RECORDING SITES 1-9 IN RELATION TO COW GREEN RESERVOIR.

GROUP A : 1, 2, 3
GROUP B : 4, 5, 6, 7
GROUP C : 8, 8B, 9



down-wind from the reservoir. Thirdly, from the relatively short period of recording since the reservoir filled (5 years), data are probably inadequate to detect true trends.

The plants have survived for several thousand years under varying conditions of climate, and it seems most likely that they will not be affected by small changes in climate _per se_, although other factors associated with the construction of the reservoir may prove to be more serious.

10.3 The effects of grazing.

There have been many references through Chapters 4-7 of the observed or putative effects of grazing on the plants in this study, and it is clear that grazing plays, and has probably always played, a major role in the survival and success of these plants. On Widdybank Fell, grazing is almost entirely by a flock of sheep whilst grazing on the study plots on Cronkley Fell is almost entirely by rabbits. Sheep-grazing is seasonal, for the warmer 8-10 months of the year only (I. Findlay, pers. comm.), while rabbit-grazing is, of course, all-the-year-round. This may, in part, account for the severe erosion on Cronkley Fell, since productivity in winter is virtually nil, and severe overgrazing (and probably high rabbit mortality) must result.

The role of grazing on the post-glacial survival of the rarities has been briefly discussed in 2.4, and its effects on the present-day vegetation only are considered here. Grazing affects the plants in the sward in a multiplicity of different ways, and the relative importance of these varies considerably according to the type of herbivore, the period and intensity of grazing, the substrate, the species available to colonise the sward, the climate, and other factors, and it is therefore hardly surprising that it is difficult to make generalisations on the effects of grazing, especially in view of the rather limited range of studies carried out.

It has been known for a considerable time that removal of herbivores from a grazed environment may lead to a reduction in plant species diversity (e.g. Tansley and Adamson, 1925; Hope-Simpson, 1940; Watt, 1960), and from a conservation point of view, such knowledge is essential. Equally, overgrazing may lead to erosion, or to dominance by a few unpalatable species, depending in part upon the situation. Jones (1933) found that continuous overgrazing where the dominants were palatable led to increased diversity, while Milton, (1940 and 1947, quoted by Harper, 1969) found that overgrazing caused dominance of a few unpalatable species. On the sugar limestone grasslands, grazing pressure is very high, relative to productivity, since the sheep congregate on the grasslands in preference to the blanket bog. The dominant species are palatable (e.g. Festuca ovina, Sesleria caerulea) and there is no evidence of increasing dominance of unpalatable species. On the rabbit-grazed summit of Cronkley Fell, it seems likely that the combination of friable soil and severe grazing in all seasons has caused the extreme erosion that occurs.

In Teesdale, Welch and Rawes (1964) have shown that reduction in grazing pressure leads initially to a reduction in species diversity, and both Doody (1975) and Bellamy (1976) have pointed out that removal of grazing on Widdybank Fell appears to lead to reduction in diversity at the expense of the rarer species. So, the preliminary and most important conclusion must be that grazing removal, at least on the deeper limestone soils, would lead to a reduction in the number and variety of the rare species which would probably be irreversible.

However, the situation is much more complex than this. Herbivores do more than remove the leaves of the plants in the turf. Observations indicate that herbivores in general create bare patches by rubbing, lying, or trampling, (Harper, 1969) which may be essential for the survival of some species. Harper (1977) quotes unpublished data from Sarukhan showing that the germination pattern of seedlings of Ranunculus bulbosus closely followed the outline of hooves of cattle-trampling in the previous year. Grazers may consistently remove flowers or fruit of plants in the turf, although at the same time they may assist dispersal of seeds that can survive passage through the gut. Further, long-term adaptations to grazing may occur with respect to reproductive strategy (as suggested for Gentiana verna in this study), palatability, growth form, and other factors. They may also remove whole plants of some species (e.g. Gentiana in this study).

It has become apparent throughout this study that the severe grazing taking place is inhibiting flower and fruit production in most species, and that a considerable number of potential new plants are lost in this way. At the same time, there is limited evidence to suggest that some species may be responding to this grazing by producing less flowers, both by long-term genetic change and through the effects of defoliation. Yet grazing appears to be essential for the maintenance of the habitat in which the rare species can survive. Thus there exists a critical balance between the level of grazing which allows such species as Primula farinosa, Viola rupestris, or Polygala amarella to produce adequate seed for replacement, and the level that allows the development of more competitive species that will oust the rarities. If all the rare species are surviving adequately, then the present management is likely to be the optimum one, with any change probably favouring some species at the expense of others. The concentration of rarities is such that it is difficult to manage for one species in isolation from others. However, the indications are that the survival of *Polygala amarella* is very precarious, and there is a good case for small-scale selective exclusion of grazing around *Polygala* plants during the flowering and fruiting season to allow an increased development of seeds. If the proposed changes taking place in the genetic constitution of the *Gentiana* clones are accepted as likely, there may also be a case for selective prevention of grazing around *Gentiana* plants in various areas, so that seed of more floriferous clones may be dispersed, and variation introduced. At the same time, care must be taken that such management changes do not alter the environment away from that demanded by *Polygala* or other species.

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