An analysis of the population dynamics of draba incana, polygala amarelle and gentiana verna in upper Teesdale

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AN ANALYSIS OF THE POPULATION DYNAMICS OF DRABA INCANA, POLYGALA AMARELLA AND GENTIANA VERNA IN UPPER TEESDALE

being a

Thesis for the Degree of Master of Science

of the

University of Durham

by

R. C. FORDHAM, B.Sc. (Dunelm)

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For Edie and Pete

ABSTRACT

The thesis outlines the ecological and conservational importance of the three species.

Nine years' demography data collected on *Draba incana*, *Polygala amarella* and *Gentiana verna* are then analysed to provide a picture of flowering performance; vegetative reproduction; establishment and recruitment; mortality patterns; age-structure and dispersal, as these processes occurred in the study populations.

The results are discussed in the light of current theories about adaptive strategies exhibited by plants.

DECLARATION

Several stages in the production of this thesis are mentioned in the acknowledgements:

1. Field recording: collection of the basic information on the plants *in situ* on the fell,

2. Preliminary data processing: the conversion of the above records into a state from which they may be analysed,

3. Analysis: the description and interpretation of the demography of the plants in question, including relating this to the current body of thought contained in the relevant literature. That is, the results and discussion sections of this thesis.

Field recording and preliminary data processing have been carried out by several people over the period of study. I have carried out the data processing stage of some field records from 1975 and all those from 1976. I did, in addition, have occasion to verify certain of the 1976 field records.

The analysis presented here is wholly my own, except where due reference is given.

No part of this work has previously been submitted by me for a degree at this, or any other, University.

R C Fordham.

R. C. Fordham

December 1978

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The main body of this thesis represents an analysis of results collected by several people over a period of nine years. This analysis would not have been possible without a great deal of effort on the part of those peopole, viz:

Ms. Maureen Watson who established the sites on Widdybank and Cronkley fells during 1968.

Mr. John Muggleton and Dr. Margaret Bradshaw who carried out the field recording in 1969.

Dr. Pat Doody who carried out recording and data processing from 1969 to 1972 (inclusive). Mr. Bob Gibbons did the same from 1972 to 1975. Mr. Peter Marren completed the 1976 field recording and processed some of the 1975 records.

Pat Doody included data from 1969 to 1972 in his doctoral thesis.

All the above work was supervised by Dr. Margaret Bradshaw.

Latterly the data processing stage was computerized by Dr. Tim Gleaves and Dr. Jane Valentine. The computer programme greatly expedited this stage, and I am most grateful to them for their help with this.

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1. THE VEGETATION OF TEESDALE

1.1 Geological Background

The dramatic landscape of upper Teesdale is due principally to the Great Whin Sill. Since its intrusion into the country-rock in late Carboniferous times this massive feature has resisted the erosion which has removed overlying rocks and the majority of the drift left behind after the retreat of the last glacier. The top of the sill and its adjacent limestones now form the plateau of Widdybank Fell and the escarpment of Cronkley Fell.[70]

Towards the end of the Carboniferous period there was a time of uplift of the country-rock. Contemporaneously with this activity, the sill was intruded. It cut across the basal limestones of the Carboniferous series, resulting in the metamorphosis of the surrounding rocks.[70]

Of particular relevance to this study are the pure, light-coloured Melmerby Scar and Robinson limestones which were metamorphosed to form a saccharoidal marble up to 25 m from their lower point of contact with the sill.[52] Subsequent erosion has exposed the Great Whin Sill and the Melmerby Scar limestone though both are, in some places, overlain by glacial drift.

The thickness of the remaining drift affects the weathering of the saccharoidal marble, and the type of soil thus produced. Where drift is at its thinnest, or the limestone itself is exposed, a combination of surface and subsurface weathering and solution has resulted in the development of rendzina soils.

Johnson <u>et al</u>.[52] consider that these soils have provided unstable and excessively drained habitats since the end of the Late Glacial and that these have provided "... a continuous series of precarious habitats suitable for the survival of the alpine plants".

It is with these soils, and the outcrops of saccharoidal marble, that the relict flora is associated today.

1.2 Vegetational History

An early debate[84] on the origin of the Teesdale flora centred on the controversy of per- against peri-glacial survival to explain the disjunct distributions of the rare Teesdale species. Willmott (op cit.) argued specifically that "it is impossible that Teesdale should produce a series of unique and peculiar habitats". Godwin[28] circumvented this argument stressing the importance of explaining the persistence of the rare species through periods inimical to their survival: an essentially historical emphasis. Recent palynological and archaeological work has evinced the theory of the survival of the flora in a succession of suitable habitats, and what follows is a summary of this.

It is probable that at the time of its maximum extension the Devensian ice-sheet completely covered Teesdale.[13] It began to retreat northwards across Britain and northern Europe sometime before 12000 years B.P., As it did so, it left in its wake uncolonized terrain consisting of superficial glacial and peri-glacial material sorted by solifluxion processes.[29] The immature soils so-formed provided a substratum of high base content in an essentially peri-glacial (though progressively warming) environment. These conditions led to the rapid expansion of the late glacial flora from the southerly refuges which it occupied at the time of the maximum extension of the ice-sheet. The rapidity of this colonization has been compared with that seen in modern times on to waste-land laid bare by industrial man.[29] This rapid spread, undoubtedly aided by the existence of land-bridges between Britain and Ireland and the European continental land mass, led to an "... extensive juxtaposition of genera, including many not afterwards found growing near together [and] formed a very interesting vegetation".[71] The extent of this, or a very similar flora, throughout lowland Britain and Europe during Late-Glacial times has been shown by the discovery of characteristic pollen assemblages in deposits dating from this period.[29] For instance, Minuartia stricta, a plant with an arctic-prealpine distribution,[15] which now has Upper Teesdale as its only British site, has been found in Late-Glacial deposits in Ireland.[76]

Palynological evidence has been used[13] to show that the fell-tops and valley floor varied in the timing of the successive vegetation types which occupied them. Chambers (op cit.) states that there is an "... indication that the climate continued to be severe in the uplands after a general amelioration had taken place in more lowland areas ..." (see section 1.3.1) and that this persisted "... well after the normal date for the Late-/Post-Glacial boundary". He describes well-preserved cryoturbation structures under the peat as evidence for this. Dating the late glacial vegetation at c.10,000 years B.P. - later than usual - he emphasises that "late glacial vegetation continued to flourish in Upper Teesdale after its replacement in more lowland parts of northern England". Thus the survival of the late glacial flora around the time of the Late-/Post-Glacial boundary was ensured by the persistence of the conditions which had allowed its initial establishment in the area.

The early Post-Glacial (up to 8,800 years B.P.) saw the migration, via the more sheltered valley floor, of hazel, birch and, to a lesser extent, pine into upper Teesdale.[102] The more thermophilous oak, alder and elm followed via the same route. Pine was never completely replaced in Teesdale, remaining up to about 6,000 years B.P., especially associated with limestone. In this context the occurrence of Carex ericetorum on the fell now is illuminating. It is taken to be an indicator of past pinewoods and is part of the ground flora of Russian pinewoods today.[102] The expansion of the more thermophilous tree species continued up to the climatic optimum (c.5,000 years B.P.). Pollen spectra from the fell top at the time of the forest maximum have 30-40% herb pollen, as compared with the 5% typical of valley sites.[102] Turner et al. (op. cit.) conclude: "although habitats for the rare species may have been more restricted than during the late glacial, development of woodland on the fell could at most only have decreased the areas available to them, certainly not destroyed them altogether".

The periglacial instability had given way to instability due to, for the most part, ground water fluctuations during the Atlantic period.[94] One can visualize processes associated with this which would maintain conditions suitable for the relict flora: erosion of peat to continually expose new areas of limestone, flushing with base-rich water; grazing and trampling of marshy areas by wild animals; the erosion of stream and riverside gravels; and waterlogging of soils leading to poor root growth of most tree species. Certain other suitable niches have probably persisted unchanged up to modern times, for instance pockets of immature soils on limestone edges and cliffs. By their very nature, all of these sites would have prevented the development of a closed tree canopy and thus would have been associated with the unshaded conditions necessary for the survival of many of the rare species. Pigott[76] summarizes: "Viola rupestris, Carex ericetorum and Dryas can certainly survive under scrub and on very small outcrops, while Polygala amara* and Gentiana verna have both been noted in fruit under small openings in the canopy of Sub-alpine Picea abies forest in the Alps". Over this period grazing by native fauna, for example, red deer,[57] would have maintained a cropped herb/grass layer which would have benefitted the survival of the relict flora by reducing

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* Polygala amarella Crantz. is now accepted as the more correct nomenclature.[24]

Other plant nomenclature follows Clapham, Tutin and Warburg,[15] except when other papers are referred to, when nomenclature follows that of the original author.

competition with grasses. This is a role later taken over by man's domestic animals: initially cattle (Bos spp.)[51] and later sheep, which are an active agent in the maintenance of the grassland communities in modern times.

Evidence has been found for the presence of man on the Moor House National Nature Reserve (to the west of upper Teesdale) from about 5,900 years B.P.[13] From this time man and his domestic animals played an increasingly important role in maintaining the variable but continuing thread of instability necessary to the survival of the relict flora.

After the climatic optimum, the change of woodland to blanket peat became irreversible,[102] and wide tracts passed over permanently to blanket peat. This process would not have occurred on freely-draining shallow soils covering the limestone. The latter exerted an influence vertically through the soil profile maintaining a high base-status in the soils. Podsolization would not, therefore, have taken place at these sites.

Woodland-to-grassland changes were reversible[102] and were probably maintained in a state of flux by the activities of Mesolithic man. Johnson[51] considers that middle stone age people "were wandering hunters and probably seasonal visitors to the high fells and dales of the Pennines". Their activities provided a limited number of grassy habitats until 2,500 years B.P. when these habitats became more extensive, associated with climatic deterioration.

Later, man's effects on the forest were more apparent and aided this removal. "Fluctuations of the herb pollen frequency on the Cow Green Reservoir Basin and Widdybank Fell diagrams suggest that small temporary clearings were being made during the Neolithic period and early Bronze Age."[13] Turner[100] considers that the Neolithic way of life persisted into the Bronze Age in this area, with pastoralism as the basic way of life. Grazing was thus established in the area. It has remained as a major factor maintaining the limestone grasslands, and the rare species, to the present day.

Squires[93] provides a concise summary of man's influence on the vegetation throughout the Post-Glacial, and recently a very readable introduction to Teesdale has been published[14] which contains chapters by Turner[101] and Roberts[82] on pre-historic and historic land-use practices which have affected the vegetation.

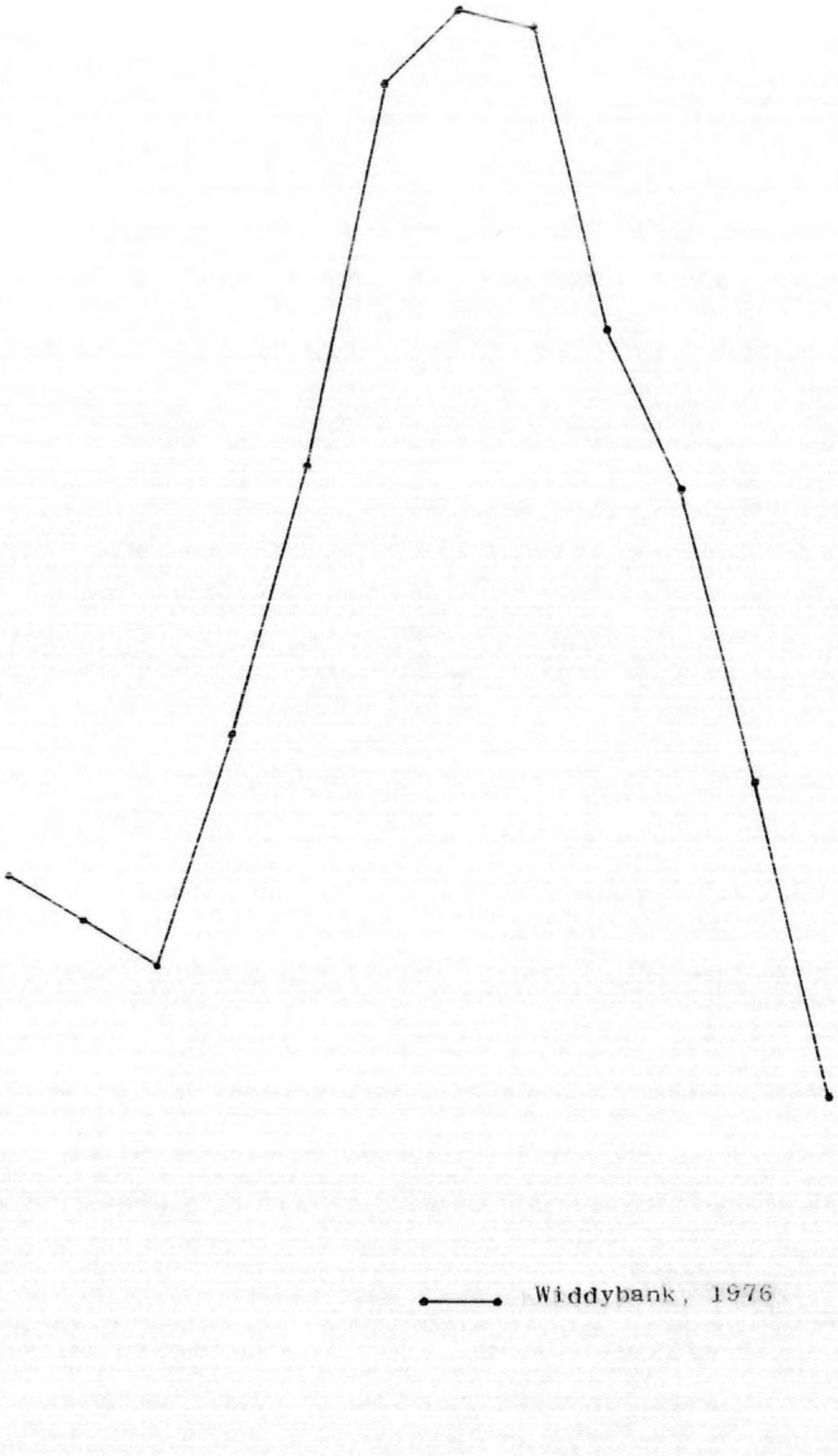
Final proof of the persistence of this flora _in situ_. is provided by the discovery of several species in pollen diagrams throughout the Post-Glacial period. Of the seventy-five rare species of flowering plants described by Pigott,[76] sixteen are identifiable by pollen at, or close to, species level. Of these, eleven have been found in Teesdale.[102] _Betula nana_ has been recorded at four sites in upper Teesdale, from pollen zones V, VI, VIIa, VIIb and VIII. In 1965 Hutchinson[49] found a few live plants on the fell with subfossil leaves in the peat beneath.

1.3 The Climate of Teesdale

Teesdale lies at latitude 54°40'N. It has a basically oceanic climate characterized by rain at all seasons, cool summers and mild winters. Since it occupies a position approximately equidistant from the North Sea and the Irish Sea (about 70 km east and west respectively) the oceanicity is marked. Superimposed on this overall picture the topography of the region causes distinct local differences. Thus, the climate of the fell tops stands in marked distinction to that of the immediately surrounding dale. Broadly, climatic patterns trend west-east across the region with the altitudinal gradient and its associated rain-shadow.

Temperature

Table 1.3.1a shows the average air temperature at three sites in the upper dale. The figures are displayed graphically in Figure 1.3.1a where the overlay allows comparison of the anomalous figures for 1976. These are


Widdybank, 1976

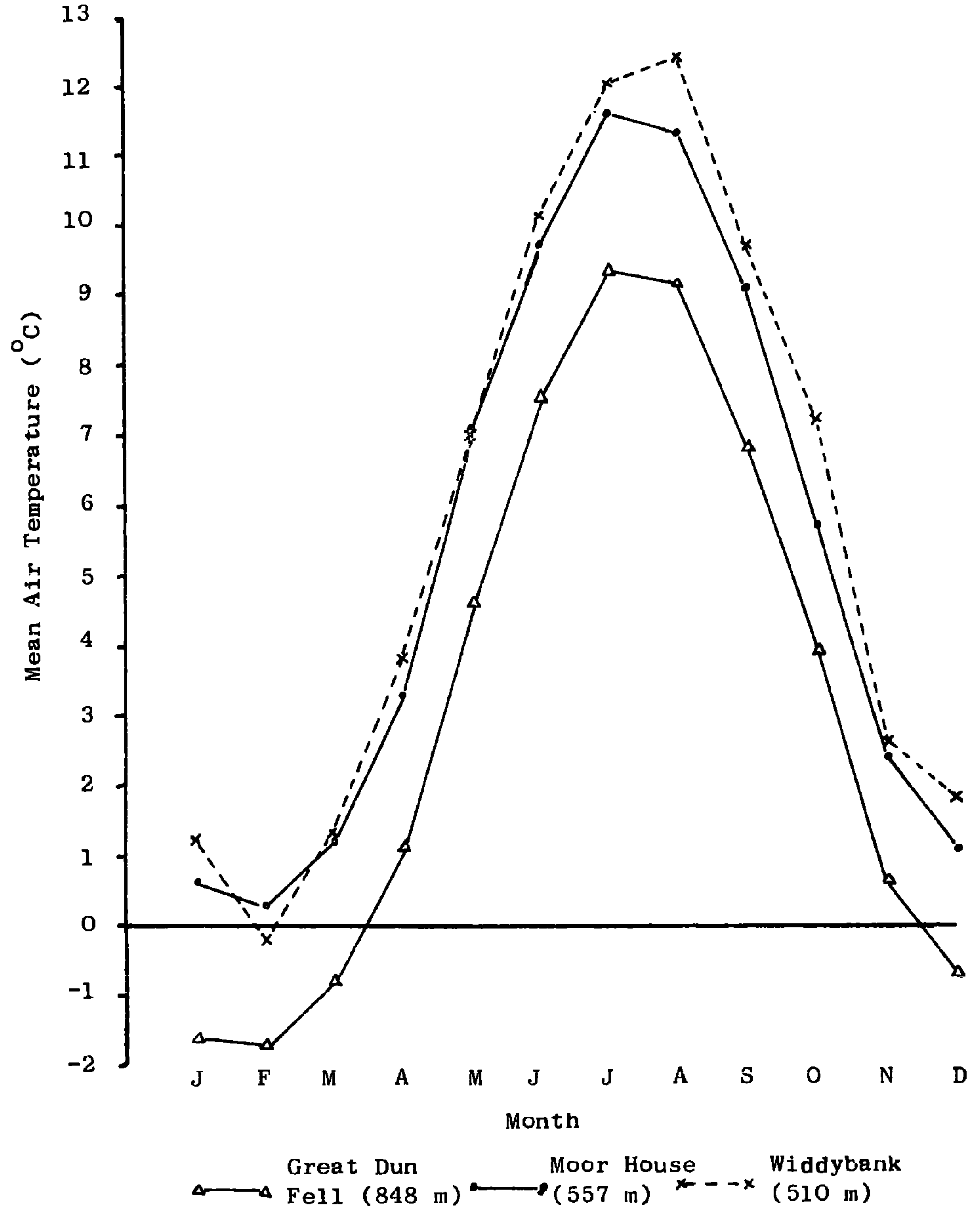


Figure 1.3.1.a : Annual pattern of variation in air temperature

relevant to later sections.

Table 1.3.1a : Mean Air Temperatures $\frac{t_{max} + t_{min}}{2}$ (^{o}C)

Month:	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Year
Great Dun Fell* (848 m)	-1.6	-1.7	-0.8	1.1	4.6	7.5	9.3	9.1	6.8	3.9	0.6	-0.7	3.2
Moor House** (557 m)	0.6	0.3	1.2	3.3	7.1	9.7	11.6	11.3	9.1	5.7	2.4	1.1	5.3
Widdybank^{+} (510 m)	1.2	-0.2	1.3	3.8	7.0	10.1	12.0	12.4	9.7	7.2	2.6	1.8	5.7
Widdybank 1976^{++}	1.9	1.3	0.7	3.8	7.4	12.5	13.5	13.3	9.2	7.1	3.2	-1.0	6.1

* recalculated from Manley (1942); period: 1906-1935.
** recalculated from Manley (1943); period: 1906-1935.
\+ data from Pigott (1978); period: 1968-1975.
++ data kindly supplied by Richard Harding, Institute of Hydrology.

Widdybank temperatures are higher than Moor House by about 0.5 C^{o} during the period October to April and by about 1.0 C^{o} for the rest of the year: a difference attributable to altitude, the Widdybank station being 47 m. lower. The warm summer of 1976 resulted in a yearly average 0.4 C^{o} higher than that for the 1968-1975 period. Once again, the greatest differences are in the summer months.

The mean diurnal range of temperature at Moor House is about three-quarters that of lowland Durham. Daily maxima are similar to the lowlands, but minima tend to be higher since cold air flows away from the fell-tops. Mean air temperatures, however do not convey the extent of freezing conditions on the fells.

Table 1.3.1b gives the numbers of frost days and days with snow cover, illustrating the bleakness of the climate. Manley[63] states that summer averages are similar to those recorded at about 1,000 m in central Norway, some ten degrees of latitude further north.

Table 1.3.1b : Frost and Snow Conditions at Moor House[64]

	Month:	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Yea
Frost days*		28	25	27	23	10	1	0	0	1	8	20	25	168
Snow covers		18	19	19	13	1	<0.1	0	0	<0.1	2	12	17	100

* days when the minimum air temperature is 0.0°C or below.

Rainfall

Annual rainfall throughout Teesdale shows a marked relationship to altitude (see Table and Figure 1.3.1c). It should be emphasised that these stations be progressively east of the Pennines and tend, therefore, to reflect the rain-shadow effect.

Table 1.3.1c : Relationship between Altitude and Rainfall* (1916-1950)

Station	Altitude (m)	Rainfall (mm per year)	Distance east of Cross Fell (km)
Cross Fell	893	2285**	-
Moor House	556	2062	5.0
Forest-in-Teesdale	372	1393	11.5
Newbiggin	271	1143	16.5
Barnard Castle	171	800	30.0
Croft Hall	31	634	54.0
Stockton	19	600	68.0

* from British Rainfall, 1967, except:
** estimated.[90]

Wind

The wetness of the fell-top environment is due to cloud build-up over the Pennines as the prevailing westerlies rise and moisture condenses. This is the usual pattern, though late spring is often characterized by polar airstreams which depress air temperatures well into May.[62]

Maximum temperatures at Moor House are consistently lower (by c. 4 C°) than in the east of the region when westerlies prevail.[62]

High winds characterize the fell-tops. Smith[90] quotes figures from 1967, a windy year, during which Durham City had five days with gale force

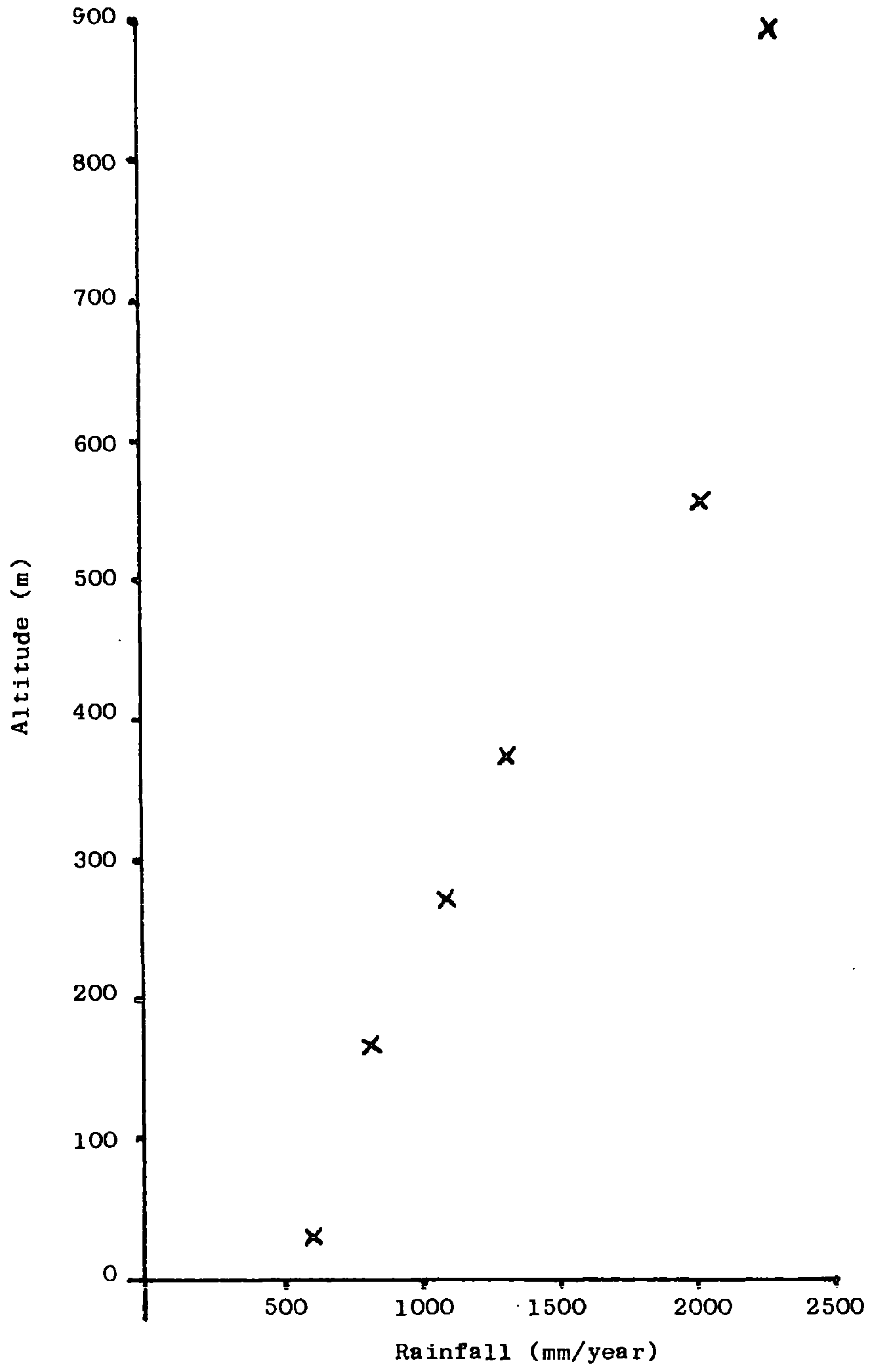


Figure 1.3.1.c : Relationship between attitude and rainfall (N.B. Stockton ommitted)

winds. This compares favourably with forty-nine at Moor House and Great Dun Fell with 127.

The mean daily duration of sunshine decreases westwards due to cloud build-up. Great Dun Fell has an average of 2.5 hours per day, and Moor House 3.3 hours per day.

Summary

Manley[62] states that "as a whole the figures confirm the prevailing impression of bleakness associated with a windy and damp upland and correspond well with records at sea-level in Southern Iceland" - a situation in which some of the Teesdale rarities grow today. It should be emphasised that it is in combination that environmental factors impinge on the biota. While not all the above appear extreme in isolation, it is their concomitant effect which is important. This is discussed in section 1.4.

1.4 Environment and Vegetation

Bradshaw and Doody[10] distinguish four habitat-types on Widdybank and Cronkley fells by their physical characteristics.

A. Open

These sites are characterized by loose uncolonized sugar-limestone sand, often with outcrops of unweathered limestone. They undergo continual erosion due to several factors. Moles have been mentioned by several authors[10,16,76] as maintaining open habitats. Due to poor vegetation-cover the surface is very fragile. Trampling by sheep, ponies and humans breaks up the existing vegetation very easily. Constant shifting of sand due to wind action makes recolonization very slow. The exclosure at Thistle Green on Cronkley Fell has been in position for eleven years and much of the surface is still bare. Rabbit scrapings and burrow entrances are often enlarged by sheep which use these features as rubbing-places.

B. Intermediate phase A

This is semi-open grassland developed on a shallow soil. Small patches of rock or base soil are to be found along with areas colonized only by mosses. Grazing and physical factors (as before) in combination with poorly developed soils maintain this type.

C. Intermediate phase B

This has developed, and is maintained principally, by grazing by sheep and rabbits. The vegetation forms an "open, not dense matrix".[10]

D. Closed with dwarf shrubs

Vegetation here is taller and denser than in C and is formed on a deep, humus-rich brown-earth soil. Grazing is important here, also. When this is relaxed, the vegetation reverts to a mosaic of tall and short patches, dependent on the locally dominant species.

The fell-tops consist of a mosaic of all these phases which Bradshaw and Doody (op. cit.) consider to be stages in a sere. Disturbances of the sort described cause local reversal of the normal seral development. The tension between the open sites (A and B above) is important in providing habitats for a number of the rarities: those least tolerant of competition, for example Draba incana. In these situations, therefore, the physical effects leading to openness are important in maintaining suitable conditions. The vegetation is a pioneer-type and inter-specific competition is unlikely to be a major factor controlling its floristic composition.

In the closed types, this is not true, however, and one must consider how it is that the rarities, many of which have low annual productivity compete successfully with the other species in the vegetation.

The underlying rock has two principal effects: moisture tensions greater than permanent wilting are experienced in most summers in bare sugar limestone soil, preventing colonization by certain species until sufficient humus has accumulated;[107] phosphate levels are moderately low in the parent rock. They are possibly limiting due to interaction with other soil constituents.[50] These two factors probably operate to weigh competitive advantage in favour of the rarities.

As has already been stated (section 1.3.1) the overall climate of upper Teesdale is comparable with the arctic, as the formation of stone stripes and stone polygons in the Moor House NNR testifies.[51] Bellamy et al.[5] found that Teesdale ecosystems have an annual dry weight shoot production of 150 g/m^2 - a typical figure for arctic and alpine vegetation - and they consider that "Teesdale ecosystems seem to have much in common with true alpine tundra ecosystems, and it seems reasonable th speculate that the critical figure of 150 g dry weight shoot production/m^2 is of more than local significance in the survival of the type of plants in question" (i.e. the rarities).

The survival of alpine species in Teesdale can be seen as part of a general trend to grow at lower altitudes further north. Both arctic and alpine species survive due to lack of competition with faster-growing plants. The latter cannot survive the rigours of the fell-top environment. The mechanism, simply stated, is as follows: the decrease in the productivity of the vegetation with altitude results from the shorter growing season and the exclusion of the more productive lowland species. Thus, the rarities, most of which are of low stature and slow growers compete successfully.

Bellamy et al. (op. cit.) summarize: upper Teesdale "... is a large-scale example of a boundary complex of vegetation types fluctuating with changes in macro- and micro-climate - a constantly varying complex unstable in detailed pattern, but stable in overall make-up ..." The effect of man and his animals is to temporarily stabilize this boundary complex leading to the existence of considerable tracts of unique vegetation.

1.5 Status

1.5.1 The Limestone Grasslands

The various plant communities of upper Teesdale were first described by Lewis[58] and later by Pigott,[76] both used an essentially non-systematic, descriptive approach. Since that time, the limestone grasslands have been included in various phytosociological studies which have allowed them to be placed within, and compared with, the continental vegetation classification.

Shimwell[89] evaluated the status of the Class *Elyno-Seslerietea* Br.-Bl. 1948 in the British Isles. This Class includes most calcareous grass heaths of the arctic-alpine regions.

In Britain a broad zone of grasslands in which *Sesleria caerulea* is dominant or co-dominant exists across northern England. These communities form a phytosociological link between the lowland grasslands of the Class *Festuco-Brometea* Br.-Bl. et R. Tx. 1943 em. R. Tx. 1961 and the Class *Elyno-Sesterietea*.

The sub-alliance *Seslerio-Mesobromion* Oberd. 1957 (short grassland) and the alliance *Caricion davallianae* Klika 1934 (flush and mire communities) contain sixty per cent of all the species of the Teesdale Assemblage. Jones[53] states that this vegetation is unique, at this level, to upper Teesdale. Of the eight Classes described by her, six have components unique to Widdybank and Cronkley Fells.

Ratcliffe[80] states that "the greatest interest ... attaches to the few communities which have no exact counterparts either in mainland Europe or elsewhere in Britain, the outstanding example being the association *Seslerio-Caricetum*". The populations making up this study are situated within this association.

The phytosociological classification of Pigott's[76] "sugar limestone grassland" may be summarized thus:

CLASS	: Festuco-Brometea
ORDER	: Brometalia erecti Br.-Bl. 1936
ALLIANCE	: Mesobromion erecti Br.-Bl. & Moor 1938 emend. Oberd. 1949
ASSOCIATION	: Seslerio-Caricetum pulicaris Shim. 1969 emend.[11]

The species under consideration are thus representatives of a vegetation type peculiar to upper Teesdale. Several of the species of the study as it was originally conceived[21] are character species at some level of the vegetation classification, viz.: Gentiana vesna, Viola rupestris, Polygala amarella, Carex ericetorum, Primula farinosa and Draba incana.[11]

1.5.2 The Teesdale Assemblage

When, in 1844, the Backhouses wrote "An account of a visit to Teesdale in the Summer of 1843",[3] the area had seen about fifty years of intensive "botanising" - the heyday of Victorian field natural history.

The earliest recorded spring gentian was "gathered in April 1797, in Teesdale Forest, Durham, by Mr. John Binks, and sent ... by the Rev. Mr. Harriman, the first botanist who ascertained it in England".[17] Thence followed a brief period of very active study so that in 1805, when "The Botanist's Guide through the Counties of Northumberland and Durham"[110] was published, almost all the Teesdale rarities had been recorded.

Records have since been added more slowly to the list. In 1965 Hutchinson discovered Betula nana on Widdybank Fell[49] (see section 1.2); and in 1975 Nigel Holmes re-found Carex aquatilis at a new site after it had been thought lost by submergence of its original site in the reservoir-basin.[45] He found, for the first time, Grimmia agassizii, a rare arctic-alpine moss, in that year.[44]

Throughout the early period a picture had emerged of a phytogeographically heterogeneous mixture of plants with disjunct distributions: the Teesdale Assemblage. Pigott[76] listed seventy-five species of flowering plant which are rare or local. Bradshaw[8] notes fifty-seven species with "some particular phytogeographical interest". Bradshaw (op. cit.) emphasised the concentration of rare species in Teesdale by enumerating those of the assemblage in the ten-kilometre aquares of the "Atlas of the British Flora".[73] That containing Cronkley and Widdybank fells, 35/82, has twelve. Square 35/83, including the north end of Widdybank fell, has seven. In the Scottish Highlands a few have five species represented, whilst others have four. In most British localities only one is present.

Elkington[23] notes that sixteen of Hulten's[47] twenty-one phytogeographical elements are represented in the Teesdale Assemblage.

Upper Teesdale represents a marginal habitat for several of the species which are at their phytogeographical limit in this area. Helianthemum canum, a plant with a continental-southern distribution, is at its most northern and highest station in Teesdale; whilst Alopecurus alpinus, a plant with a circumpolar distribution, is at its most southerly station.

The marginal nature of the environment has probably resulted in the local extinction of some of the rare plants. Turner et al., discussing the likelihood of encountering pollen of the rare plants state: "when one considers that within an area of about 6 km^2 we have only looked at a small sample of the pollen falling on as little as 20 cm^2 peat it is really rather surprising that any rare species pollen has been found at all".[102] This tends to suggest that at one time the rare plants were much more widespread than they are at present. It is possible that the habitat-instability leads to local extinction proceeding more rapidly than re-establishment for certain of the species. Thus, Turner et al. (op. cit.) state that pollen analysis "indicates that Helianthemum canum, which today grows only on the top of Cronkley Fell was probably growing on Widdybank too in the past". Dryas octopetala grows only on Cronkley and Minuartia stricta, Viola rupestris and some bryophytes, for instance Rhytidium rugosium, are limited, in Teesdale, to Widdybank Fell. The very local population of the blue-flowered race of Polygala amarella on Cronkley Fell has undergone a serious decline in numbers over the past few years, probably due to grazing by rabbits. It is likely to become extinct unless the strict conservation measures now imposed are successful.

Pigott[76] points out that several species in Teesdale are represented by local races. Dryas octopetala growing on Cronkley Fell is a small-leaved variety. Details of the species of this study follow in section 1.5.3.

The first official recognition of the area is contained in a report of the Wild Life Conservation Special Committee of the then Ministry of Town and Country Planning, published in July 1947.[65] This document formed the basis of the reserve acquisition programme started by the Nature Conservancy in 1949. In his "Nature Conservation Review",[79] Derek Ratcliffe refers to the Upper Teesdale NNR (established as a result of this programme) as "one of the most outstanding upland areas in Britain".

In 1975 Polygala amarella and Gentiana verna were given formal, legal protection with the passing of "The Conservation of Wild Creatures and Wild Plants Act".

1.5.3 The Species Studied

Fearn[24] states that Polygala amarella "is exceedingly rare in this country, consisting of approximately 18 populations many of which contain fewer than 30 individuals". These populations are found in four disjunct areas, one of which is Teesdale. In 1970 the number of individuals in this population was estimated at between 1,500 and 2,000 individuals (Bradshaw and Doody, in press). The species is recorded as endangered by Perring and Farrell.[72]

There is little intra-area variation, though quite large differences between areas, suggesting a long period of isolation. Teesdale plants are most similar to those found in Scandinavia.[24] They are polycarpic.

In Teesdale pink- and blue-flowered types are found. Both occur on Cronkley, whilst only blue-flowered individuals are found on Widdybank Fell.

Perring and Farrell[72] summarize the status of Gentiana verna as: "... reasonably widespread and abundant, around 55 populations being known in Britain and at least 27 in Ireland". It is confined to limestone vegetation in both areas - Teesdale in Britain and the Burren in Ireland. It is a small, evergreen, rosulate herb. New individuals grow from stolons produced by established plants. These have been found up to 15 cm long on Widdybank Fell,[22] and up to 25 cm in cultivation in Durham (Gibbons, in prep.). Elkington (op. cit.), states that plants taken from the fell live up to four years in cultivation. Individuals may be polycarpic.

Draba incana is the commonest and most widespread of the three species of this study, having sites in England, Wales, Scotland and Ireland. Under favourable conditions, for example in cultivation on sugar-limestone soil in Durham, it is biennial. In Teesdale it is perennial since the short growing season slows development to maturity. It is usually monocarpic, though dead, dry fruiting plants may remain in. situ. for several months.

1.6 Summary

The Teesdale rarities represent a relict flora dating from the Late-Glacial period. They survive in upper Teesdale due to the interaction of natural and anthropogenic environmental factors. Local extinction of some of the species is possibly common, survival for those species being dependant on the reproductive strategies of the plants coping with a marginal habitat.

Such a concentration of rare and local species growing under arctic conditions in Britain is of inestimable value to conservation and ecology.

2. METHODS

2.1 Field Records and Preliminary Processing

This summary is condensed from Doody,[21] with additions for work carried out since his study was completed.

In July 1968 nine broad regions at increasing distance from the top water-level of the Cow Green reservoir were identified on Widdybank Fell. These are the sites numbered 1-9 by Doody. In addition a site was established on Cronkley Fell, about 3 km east south-east. This is site 10. At each of these sites permanent quadrats and sample sites were established.

Permanent quadrats

These quadrats are fixed precisely, enabling the plants within to be identified by a co-ordinate. At the beginning of the study period all the individuals of the species in question present in the quadrat were noted: the original, mixed-age population. Recording was subsequently carried out in spring (April, May and June), summer (July and August) and autumn (September, October and November). Each time the quadrat was visited the fate of the plants within was recorded, and new additions were noted. These raw data constitute the basis of the analysis of the behaviour of the populations. Individuals within the population are aggregated into seasonal and annual cohorts, site groupings and others as befits the topics covered in the results section. Explanations, where necessary, are given there.

The ages of all plants becoming established since the study began, their reproductive performance and individual life-histories are thus known.

Sample sites

These have been visited less frequently than the permanent quadrats, their purpose being to provide information on the reproductive capabilities of the species in question by including a larger number of individuals than that in the permanent quadrats. It would have been impossible to obtain such information from the permanent plots without seriously affecting the behaviour of the plants therein. All individuals were counted. Those flowering were noted, along with numbers of buds, flowers and fruits per plant. Fruits were collected, in order that seed production could be estimated, in most years. Details, where appropriate, are included in the relevant results sections.

Germination experiments

Fell-top, lowland (Durham) and laboratory experiments have been carried out on seeds of Draba incana collected from sample sites on Cronkley and Widdybank fells. Previous, unpublished work on other species is also included.

Data processing

Each species may be represented in several permanent quadrats. Usually the records of all the individuals of one species in several quadrats have been amalgamated to give a larger sample: the population of this study. The records of individuals are compiled manually into cohorts dependant on the season of establishment within quadrats. A computer programme compiles these seasonal cohorts into overall seasonal and annual cohorts for the population. The programme performs preliminary calculations on seasonal and annual mortality within cohorts. It also lists sub-totals of seedlings and vegetative additions within seasons and years. These are the data upon which most of the results sections is based.

2.2 Introduction to Results and Discussion

Individuals are lost from a population with time. This may be associated with qualitative changes in the habit of the plant and therefore concentrated into a relatively short period, or it may be continuous, being related to ever-present environmental pressures. Usually the two interact.

Thus the potential to reproduce is only realized by a few of those individuals originally making up a cohort. The results sections are organized, as far as is logically possible, to follow this progressive loss, as revealed by work over the whole of the study period.

The discussion sections mirror this organization and provide comparisons with the literature. It is hoped to provide as complete a picture of the life-cycle and adaptive strategy of the three species as is at present available.

Plant demography necessitates careful definition of certain population parameters. This is provided in section 4. These terms are used strictly throughout the results and discussion sections.

In deciding how to present the data, two linked problems emerged:

1. The necessity to provide a large enough sample size so that (for example) dwindling cohorts can be analysed over the maximum time-span, and
2. Providing an adequate description of the variability of the populations of the three species over the whole of the study area.

Throughout most of this thesis the permanent plot records are lumped to provide as large a sample as possible for information on mortality, recruitment age-structure, etc. This process does not allow between-site comparisons of population parameters to be made. A full description of this variability is provided by Gibbons (in prep.) who elaborates detailed comparisons of the behaviour of the populations in their respective permanent plots.

The analysis presented here is basically descriptive, enumerating the changes which have taken place over the study period.

It is difficult and misleading to relate the reproductive performance of plants in the sample sites to the behaviour of the populations in the permanent plots (see section 9), as has been done in the past.[10,21] All permanent plots and sample sites are best regarded as samples of subpopulations of the total fell population for each species. This great variability is an inherent feature of plant dispersion patterns in nature, and it is essential to take this into consideration if extrapolations are to be made from the study populations to the behaviour of the plants over the fell as a whole.

In the following sections reproductive data came solely from sample sites and population data from permanent plot records.

Polygala amarella is represented as two populations, one established on Widdybank Fell and the other on Cronkley. They are of the blue- and pink-flowered varieties respectively. The Cronkley populations consist of one permanent plot and one sample site, whilst those on Widdybank have three permanent plots and two sample sites.

Reproductive data for Draba, only, is available from both fells. These are treated separately. Three permanent plots were established on Widdybank Fell.

Reproductive and population data for the gentian came from Widdybank Fell, where five sample sites and five permanent plots were sited.

3. DEFINITIONS

3.1 The Functional Unit of the Population

"What do I count?" This simple question precedes any demographic study. It has undoubtedly proved difficult to answer for plant population dynamicists.

Harper[35] pointed out that "two interlinked properties of higher plants have hindered the development of plant demography - plasticity and vegetative reproduction". The establishment of a basic unit to be counted is therefore a problem.

Doody[21] defined the individuals to be counted as "units of reproduction".

Both Draba incana and Polygala amarella reproduce only by seed. The plant developing from that seed has been counted as one individual. In both these species the commonest unit in the population is a distinct, rooted rosette. The aerial parts of the plant occasionally proliferate, particularly after damage to the terminal bud (e.g. by grazing). Under the conditions on the fell, this is more common in Polygala than Draba. In the laboratory and in the field spontaneously arising subsidiary rosettes have been seen in Draba incana. These sometimes produce an inflorescence analogous to that of the main rosette, but are always parasitic on the original rosette, never forming a separate root-system.

Gentiana verna produces discrete rosettes vegetatively. These are the individuals of the gentian population. They have rarely been observed to react to damage as the previous two, and this has never occurred in the study population. Fertile seeds are produced on the fell, but only three seedlings have been observed over the entire study period. The individual arising from seed is morphologically and functionally similar to that produced by vegetative reproduction.

In all three cases, therefore, the plants produce a morphological and functional unit which is readily distinguished as such, and which forms a logical starting-point for a demographic study. These individuals are morphologically fairly canalized and do not require enumeration (as proposed by Harper and White)[38] of their constituent parts to arrive at a meaningful description of the unit. It is for this reason that these three species have been selected from the eight studied by Doody.[21]

Since all three species have, as the functional unit of the population, an (usually) unelaborated rosette, they have a similar starting point for comparison of their life-cycle strategies.

3.2 Glossary

Cohort	-	A group of individuals becoming established in the population within a defined period of time, usually one growing season.
Depletion curve	-	The curve of numbers against time which describes the progressive loss of individuals from a mixed-age population.[36]
Genet	-	An individual arising from a zygote.[54]
Individual	-	The most commonly repeated functional unit of the population. Defined for the species of this study above, see also section 9.1.
Population	-	This is defined spatially in the present work as those plants within the permanent plots and sample sites, see also section 2.2. This restriction is not imposed where such topics as "the seed population" are under consideration.
Ramet	-	An individual arising by vegetative reproduction of the genet.54
Survivorship curve	-	The curve of numbers against time which describes the progressive loss of individuals within a cohort.36

4. GERMINATION AND ESTABLISHMENT

4.1 The Seed Population

4.1.1 Seed Development

No observations have been made on the development of seed from ovules in Polygala amarella.

Draba incana

The procedure adopted for Draba incana enabled observations on three (somewhat arbitrarily) defined stages in seed development. Ripe capsules were collected from sample sites (see section 2.1) on Widdybank and Cronkley fells. They had not dehisced at the time of collection, and were kept dry in the lab prior to examination to prevent germination. Capsules were split longitudinally along the natural abscission line, and the valves removed. This exposed the false septum and replum, to which the seeds and ovules are attached by a funicle. The three categories observed were as follows:

1. Ovule - a tiny (c. 0.1 mm diameter) white fragment of tissue, shrivelled in the ripe capsule. This stage could include fertilized ovules which have aborted immediately post-fertilization.
2. Non-viable seed - although critical experiments were not carried out on seed development, it was assumed that ovules after fertilization rapidly develop the brown colour characteristic of mature viable seed since this appeared as a preliminary qualitative change before the continuum of size observed in developing seeds. These are usually smaller than viable seed, and are always shrivelled and wrinkled.
3. Viable seed - large, rounded brown seeds.

With practice, the distinction between viable and non-viable seed is readily made. Attempts to germinate seeds which had been visually identified as non-viable were unsuccessful.

It should be emphasised that the above three categories are artificial, having been ascribed after observations of mature capsules. While ovules and viable seeds represent opposite ends of a continuum of seed development, category two is heterogeneous, containing all non-viable seeds. As such, it includes:

(a) seeds which did not mature,

(b) seeds which did mature, and have subsequently died.

Taken together the three categories do evaluate numerically the loss of reproductive potential during seed maturation. Causes have been impossible to ascribe.

Draba incana sample sites at 2,8 and 10 were visited in July every year to collect ripe capsules. Initially this was done to count seeds (viable plus non-viable above). These data appear in section 4.1.3. During the last two years of the study period information on seed development and viability has been collected. This is presented in Table 4.1.1a. The distinction between viable and non-viable seeds was not made with the 1976 sample.

Since flowering and fruiting vary between sites and between years the sample size (total number of capsules) is variable.

One ripe capsule was taken from (up to) 30 different individuals.

Assuming no ovules were overlooked during examination, the total for each capsule is the maximum potential seed production per capsule. This has been attained, for example, by capsules numbered 3, 4 and 5 from the 1977 site 2 sample.

There is no difference between the total number of ovules produced by plants at site 2 in 1976 and 1977 (median test; $X^2 = 0.0116$; d.f. = 1; $p > 0.8$).

Cronkley plants tend to produce a greater number of ovules than those on Widdybank (median test; $X^2 = 2.8048$; d.f. = 1; $0.1 > p > 0.05$). While the p-value is outside the range conventionally considered significant,

Table 4.1.1.a : Comparison of seed development of Draba incana in capsules from Widdybank and Cronkley fells.
(Number per capsule)

	WIDDYBANK FELL Site 2, 1976			WIDDYBANK FELL Site 2, 1977				WIDDYBANK FELL Site 8, 1977				CRONKLEY Site 10, 1977			
Capsule number (n)	Ovules	Non-viable and viable	Total	Ovules	Viable	Non-viable	Total	Ovules	Viable	Non-viable	Total	Ovules	Viable	Non-viable	Total
1	2	20	22	3	16	1	20	2	18	0	20	15	0	8	23
2	2	25	27	1	18	1	20	2	24	0	26	6	0	14	20
3	2	17	19	0	19	0	19	3	17	0	20	3	0	19	22
4	3	16	19	0	18	0	18	6	20	0	26	0	0	28	28
5	2	17	19	0	23	0	23	8	9	1	18	1	0	23	24
6	9	9	18	1	17	0	18	3	15	0	18	2	1	18	21
7	0	18	18	2	12	0	14	2	17	0	19	10	0	11	21
8	0	20	20	6	10	0	16					0	0	19	19
9	0	20	20	1	21	0	22					0	2	20	22
10	1	23	24	5	11	0	16					0	7	22	29
11	0	21	21	7	8	0	15					8	0	11	19
12	0	20	20	3	20	0	23					11	1	8	20
13	0	18	18	0	24	0	24					2	0	20	22
14	0	26	26	0	14	1	15					7	4	9	20
15	0	17	17	0	19	1	20					0	0	26	26
16	3	6	9	15	0	6	21					5	6	11	22
17	2	16	18	14	2	5	21					0	0	11	11
18	2	20	22	15	0	6	21					5	2	12	19
19	1	19	20	0	0	15	15					2	20	0	22
20	2	19	21	10	0	10	20					1	17	4	22
21	2	18	20	14	1	7	22					2	14	7	23
22	6	10	16	4	1	14	19					1	0	24	25
23	1	22	23	1	11	8	20					7	0	13	20
24	0	25	25	8	8	0	16					8	0	12	20
25	0	23	23	15	1	5	21					15	0	6	21
26				0	13	7	20					2	0	25	27
27												2	3	19	24
28												0	0	21	21

continued ...

Table 4.1.1.a (continued)

	WIDDYBANK FELL Site 2, 1976			WIDDYBANK FELL Site 2, 1977				WIDDYBANK FELL Site 8, 1977				CRONKLEY Site 10, 1977			
	Ovules	Non-viable and viable	Total	Ovules	Viable	Non-viable	Total	Ovules	Viable	Non-viable	Total	Ovules	Viable	Non-viable	Total
Means	1.60	18.60	20.20	4.81	11.04	3.35	19.19	3.71	17.14	0.14	21.00	4.11	2.75	15.04	21.89
St. error	0.42	0.96	0.72	1.10	1.61	0.89	0.55	0.89	1.74	0.14	1.33	0.85	1.02	1.38	0.65
St. dev.	2.10	4.79	3.64	5.60	8.20	4.55	2.81	2.36	4.60	0.38	3.51	4.50	5.42	7.30	3.42
Viable & non-viable															
Mean					14.38								17.79		
St. error					1.14								1.18		
st. dev.					5.80								6.25		

there is some indication that plants at site 10 have a greater maximum potential than those at site 2.

In 1977, however, plants at site 2 had more ovules develop successfully into viable seeds than those from site 10 (median test; $X^2 = 8.9036$; d.f. = 1; $0.005 > p > 0.001$).

The correlation between the number of unfertilized ovules and the total number of viable and non-viable seeds is shown on Figure 4.1.1.a. The variability in the numbers of unfertilized ovules and seeds in the ripe capsule is negatively correlated. That is, a compensatory effect links these two values. The total number of ovules produced is less variable than number of fertilized seeds, hence the variability in seed output is due, in the main, to factors operating after the formation of ovules in the developing capsule.

Regression lines have not been fitted to the points since the two values are interdependant and therefore each set of data has two solutions.

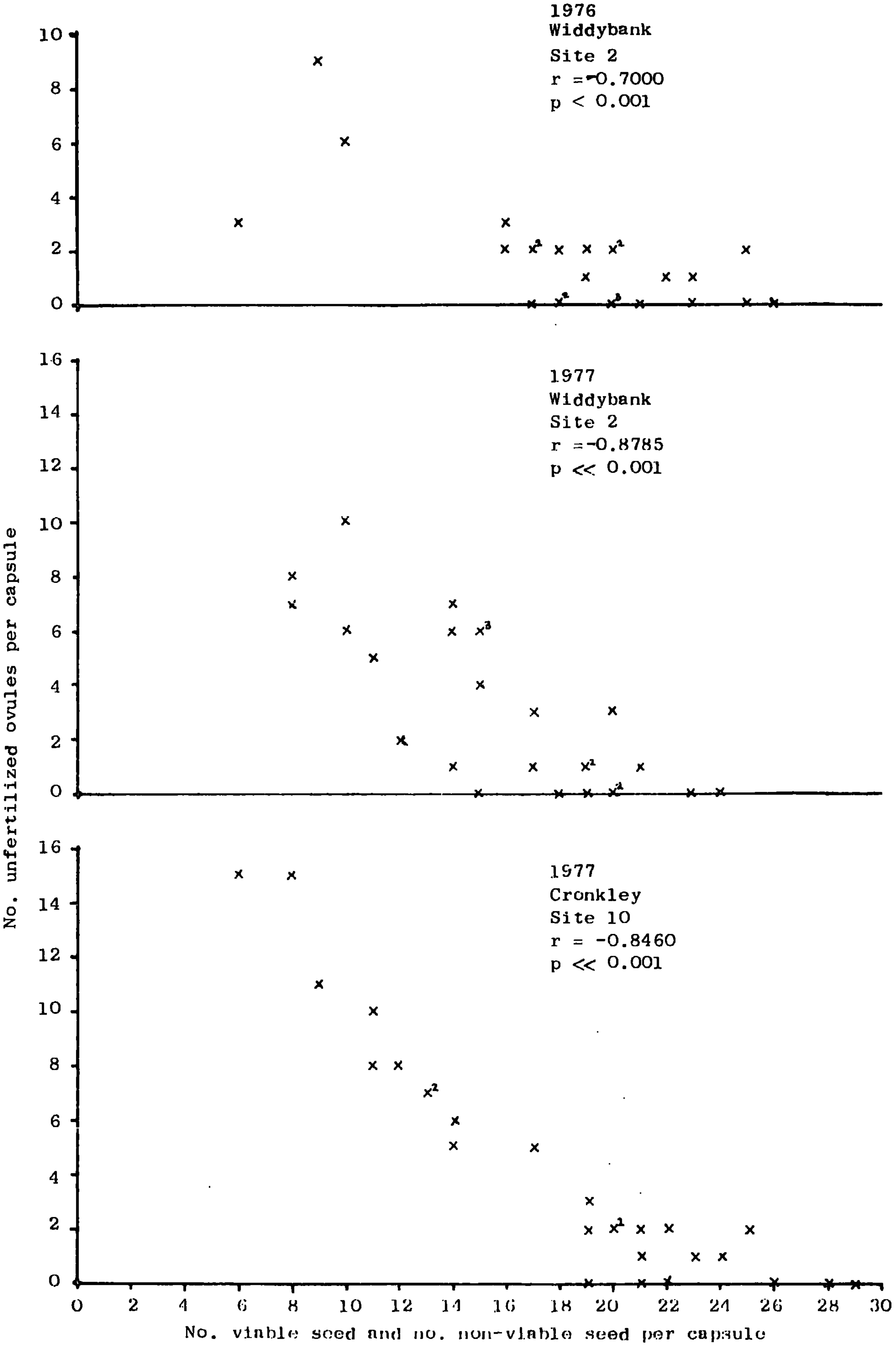
Gentiana verna

The method for Gentiana verna was essentially the same as that for Draba incana. I am very grateful to Ms. Beth Tilling for carrying out this painstaking work.

The results are expressed in Table 4.1.1.b.

All capsules were collected from an exclosure on Widdybank fell, when ripe, in 1976.

There is no correlation between the ovule number and the number of fertilized seed in these data. Unlike Draba, therefore, the total number of ovules does not determine a constant "ceiling" for maximum reproductive potential, but is, in itself, a variable quantity. Factors operating at the time of ovule formation therefore play an important role in determining the eventual number of seeds set in this species.



<u>Figure 4.1.1.a</u> : Correlation of ovule number with seed number. (<u>Draba incana</u>)

Table 4.1.1.b : Production of viable seed by Gentiana verna on Widdybank Fell (after Tilling, unpubl.)

Capsule number (n)	Ovules	Non-viable seeds	Viable seeds	Total
1	10	18	102	130
2	6	23	98	121
3	8	23	67	98
4	10	21	52	83
5	14	39	130	183
6	*50+	12	38	*100+
7	*70+	40	179	*289+
8	*80+	27	216	*323+
9	8	64	178	250
10	5	4	250	259
11	14	4	121	139
12	58	3	148	209
13	49	39	138	226
14	36	3	137	176
Mean	*29.86	22.86	132.43	*184.71
St. Error	7.10	4.79	16.11	20.48

* underestimate due to all ovules not being counted.

4.1.2 Seed Size

(a) Weight

No information is available on the weight of seeds of Gentiana verna.

A random sample of Polygala amarella seeds (122 in all) taken from Widdybank Fell in 1972, 1973 and 1974 was weighed, giving a mean weight per seed of 0.86 mg (Marren, unpubl.).

Seeds of Draba incana have been weighed, as follows:

Year	Site	Total No. Seed	Mean wt. per seed (mg)
*1968	Widdybank	100	0.16
**1976	2	466	0.11
1976	10	50	0.19

* site unknown (Muggleton, unpublished)
** Marren, unpublished.

(b) Shape

Polygala - usually very constant; like a miniature rugby-football; length 2mm, diameter 1 mm.

Gentiana - oblong; variable outline; flattened; longest axis c. 0.8 mm.

Draba - oval; compressed laterally; very variable (especially smaller seeds).

Random samples of seeds from plants in sample sites 2, 8 and 10 were compared. For each of 50 seeds, the longest axis (length) and shortest axis (width) was measured using an eyepiece micrometer and 30x magnification. The product of these two measurements (area index) was calculated for each seed. The results are given in Table 4.1.2.a.

Table 4.1.2.a : Variation in Seed Area Index of Draba incana on Widdybank and Cronkley Fells (all seeds collected in 1976).

Site	Sample Size	Mean Length (mm ± 1 S.E.)	Mean Width (mm ± 1 S.E.)	Mean Area Index (mm^2 ± 1 S.E.)
2	50	0.89 ± 0.01	0.59 ± 0.01	0.53 ± 0.01
8	50	0.91 ± 0.02	0.58 ± 0.01	0.53 ± 0.02
10	50	0.99 ± 0.02	0.63 ± 0.01	0.63 ± 0.02

The two samples from Widdybank Fell (2 and 8) were combined and compared with the Cronkley Fell sample (site 10). The latter are significantly larger. Area index was used as the size measurement (median test; X^2 = 6.7608; d.f. = 1; $0.01 > p > 0.005$).

(c) Frequency Distribution of Seed Size

Seed from capsules collected in 1976 were not sorted into viable and non-viable groups at the time of examination of individual capsules. However, subsequent germination experiments on this seed show almost 100% to be viable (see section 4.2.3).

All seeds were lumped together according to the sample site from which the capsules were gathered, then fifty were taken randomly from each and

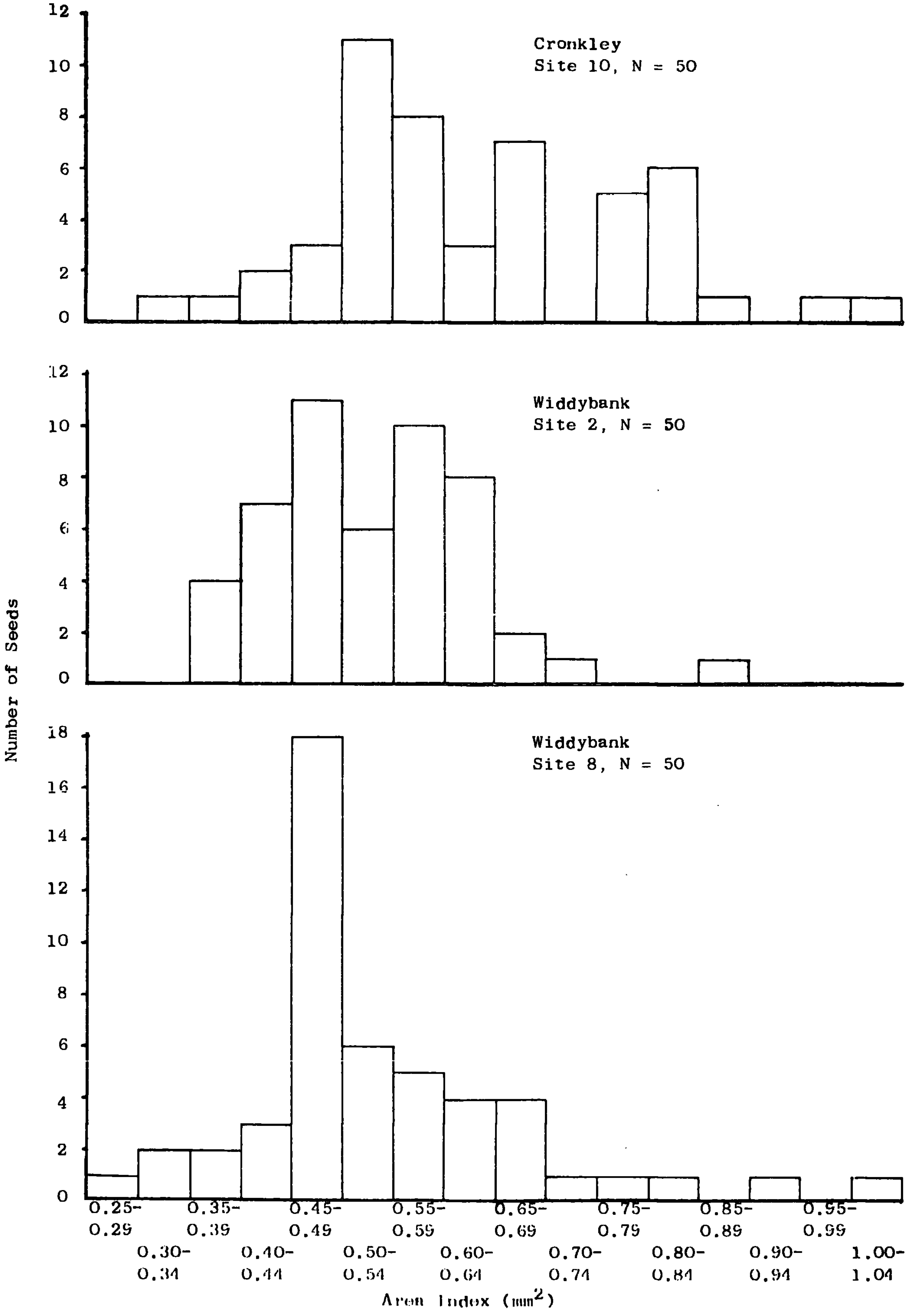


Figure 4.1.2.c : Draba incana. Frequency distribution of seed area index (all seed collected in 1976).

measured as before.

Figure 4.1.2.c shows the frequency distribution of seed size (measured by area index) of seed from the two sample sites on Widdybank Fell, and that on Cronkley. Seed from the two Widdybank sites share the same commonest size class, whilst that of the Cronkley is larger. Larger size-classes make up a generally greater proportion of the total Cronkley seed population. It is somewhat surprising that the most variable seed population, that from site 8, also has a higher maximum in one size class.

The site 2 and site 10 seed populations, while broadly lognormal, have a suggestion of a bi-modal frequency distribution (this appears in seed from all three sites if seed length only is plotted). This may suggest two phases in seed growth, perhaps related to embryo and food store, or embryo and seed-coat. If this were the case one would expect this to influence germination success and/or longevity in the soil. The more strongly lognormal distribution of seed size in the site 8 sample is some indication that any apparent bimodality in the other two may be an artefact.

4.1.3 Seed Number per Capsule - Summary

Capsules have been collected for all three species over most of the study period. In each case sample sites have remained constant, hence comparisons between years are valid. These data are presented in Table 4.1.3.a.

Elkington[22] gives the total seed production per capsule for Gentiana verna on Widdybank Fell as 113 ± 20. He gives that of a population from Ballyvaghan, Co. Clare as 379 ± 20 and notes that under glasshouse conditions plants from both populations produce the same number of seeds per capsule. An environmental effect (probably temperature) cannot, therefore, be discounted.

Doody[21] has noted that individuals of Bombus lucorum visit flowers of gentian on both fells. These often gain nectar "illegally" by biting through the calyx and corolla. This may fail to bring about pollination,

Table 4.1.3.a : Total seed production by the three species over the study period (per capsule).

	Draba incana						Polygala amarella						Gentiana verna		
	CRONKLEY			WIDDYBANK			CRONKLEY (Pink)			WIDDYBANK (Blue)			WIDDYBANK		
	Mean	Standard error	n	Mean	Standard error	n	Mean	Standard error	n	Mean	Standard error	n	Mean	Standard error	n
1969	-	-	-	17.30	0.42	48	-	-	-	1.48	0.12	23	-	-	-
1970	18.26	0.90	30	18.04	0.68	48	-	-	-	1.71	0.14	24	143.07	11.47	14
1971	19.93	0.51	30	19.90	0.38	61	-	-	-	1.80	0.16	30	132.17	19.81	12
1972	19.93	0.43	29	17.90	0.80	52	1.90	0.16	27	1.80	0.16	24	181.72	10.94	25
1973	18.03	0.76	29	17.02	0.88	45	-	-	-	1.55	0.11	20	127.00	26.29	4
1974	12.80	0.80	15	15.49	0.61	45	1.39	0.09	31	1.50	0.09	30	205.43	21.26	7
1975	-	-	-	14.09	0.34	45	1.29	0.18	7	1.33	0.07	40	126.00	53.00	2
1976	*21.20	0.93	23	*18.44	0.61	48	-	-	-	1.87	0.04	61	155.29	17.44	14
1977	**21.89	0.65	28	**19.38	0.50	42	-	-	-	-	-	-	-	-	-
Overall	18.9			17.5			1.5			1.6			153.0		

* difference : median test; $X^2 = 4.4391$; d.f. = 1; $0.05 > p > 0.02$.

** difference : median test; $X^2 = 4.2893$; d.f. = 1; $0.05 > p > 0.02$.

? Lo ovules per plant.

and also result in poor capsule development.

Factors influencing the number of seed set in gentian are, therefore, various, operating on ovule number, pollen transfer and seed development.

This contrasts markedly with Draba incana which is capable of auto self-fertilization, and normally does so.[23] This species appears to be affected by factors operating during the period of seed development, in the main. Relatively few ovules remain unfertilized, the greatest difference occurring between viable and non-viable seed numbers (compare Widdybank and Cronkley fells, 1977, Table 4.1.1.a).

The spatial and temporal heterogeneity of all facets of reproductive performance is discussed in section 9.1 in connection with flowering percentage and survivorship of buds, flowers and fruits. Seed production is similarly affected, though probably, on a per capsule basis, to a far less extent. Nonetheless, overall seed production figures should be treated with some caution since the data from which they are calculated is so variable. In view of this, standard errors would be misleading, and have not been given. The overall figures in Table 4.1.3.a are not true means.

The overall strategies of seed production of the three species differ markedly. Polygala produces a small number of large, heavy seeds (maximum of two per capsule) whilst gentian can produce large numbers of small, light seeds. Draba is intermediate between the two.

Consistent differences appear between the Cronkley and Widdybank Draba populations. The Cronkley population produces a greater number of seeds per capsule (see Table 4.1.3.a for statistics). In 1977 these were mostly non-viable, but this is not a common occurrence (Gibbons, pers. comm.), the Cronkley population usually achieving a better set of viable seed. The number of seeds produced by both populations tends to vary similarly between years, suggesting an overall climatic control.

The very small numbers in the populations of Polygala on both fells have precluded any interference with seed and capsules to the extent that comparisons may not be made due to lack of data.

It is appropriate to state here that, on both Widdybank and Cronkley fells, gentian reproduces effectively only by vegetative means, i.e. by the production of ramets (see section 4.2.2). This stage in the life-cycle of gentian is discussed, along with that of seedling establishment in Draba and Polygala, in section 4.3.

4.2 Germination

4.2.1 Pre-conditions for Germination

Gentiana verna (after Elkington)[22]

No germination if kept in a warm greenhouse. This species requires frosting before it will germinate. Cites Kinzel[55] as finding that both frost and illumination are necessary for successful germination.

Polygala amarella

Will germinate immediately after seed set if kept in a warm greenhouse. Germinate abruptly on filter-paper in the lab. Light necessary. Freezing delays germination and causes abruptness to disappear (Doody, unpubl.).

4.2.2 Observed Germination on the Fell

Gentiana verna

Over the whole period of study, only three plants have been recruited to the population from seed (Gibbons, in prep.). Recruitment via germination thus appears to be of negligible importance to the Widdybank and Cronkley populations. Nothing is known about the seasonal pattern of germination on the fell.

Polygala amarella

Germination has been recorded on the fell in every month from May to September, though few seeds germinate after the end of July. In the first half of the study period greater numbers of seed germinated in the permanent plots and it was possible to identify particularly favourable intervals.[21] In the latter part of the study period the total number of seeds germinating has been less and no favourable interval was obvious (see section 5.1). Low temperatures on the fell normally prevent germination immediately after seed-set under natural conditions.

Draba incana

Germination occurs rapidly in spring, the exact time being dependent on the duration of cold weather. Usually it is completed by the end of April, but in 1970, when this month was cold germination did not take place until the first week in May.[21] Seedlings have been observed to germinate in autumn, presumably due to newly set seed encountering suitable conditions. This has only been seen in one year, however, and may not be a common occurrence. Low temperatures presumably prevent germination in this species also.

4.2.3 Germination Experiments

A. Laboratory

This section refers only to Draba incana. The method for all experiments was as follows.

Two sheets of filter-paper were used to cover the bottom of a plastic petri-dish. These were moistened with distilled water. The required number of seeds was spread evenly over the surface of the filter-paper. The lid was replaced. Water was added throughout the duration of the experiment to keep the seeds moist. Petri-dishes were then placed in the light on a bench-top in the laboratory. No attempt was made to standardize temperature, light/dark regime or water tension. The petri-dishes were randomized on the bench to counteract any small-scale variability in conditions which may have been present.

Each set of petri-dish plus seeds constitutes one replicate.

Comparisons have only been made between replicates sown at the same time.

Seeds collected from sample sites 2 and 8 were mixed together: the Widdybank seed population. Cronkley seeds were from the single sample site on that fell. Within these two categories, all seeds were pooled and samples were withdrawn for the experiments.

Deviations from this procedure are noted where relevant.

Seed size and germination success

Experiments carried out in 1976 on seeds collected in 1973 showed that larger-sized seed germinate more rapidly and with a higher final percentage success-rate than smaller seed (Marren unpubl.). Marren's percentages have been re-expressed in Table 4.2.3.a. The results are significant ($X^2 = 18.6109$; d.f. = 2; $0.001 > p$).

Table 4.2.3.a : Seed germination related to seed size I seed number

Seed size	Germinating	Not-germinating	Total
Large	31	12	43
Medium	46	54	100
Small	33	67	100
Totals	110	133	243
Overall percentage	45.26%		

An attempt was made to repeat this experiment. Only medium and small size-classes (equivalent dimensions to Marren's) were used. Each size class and each fell was represented by four replicates of fiteen seeds in each. The occurrence of the first split in the testa was used to signify successful germination. All seeds which achieved this went on to complete germination, successfully withdrawing and raising the cotyledons. Results are summarized in Table 4.2.3.b.

Table 4.2.3.b : Seed germination related to seed size II

Days after sowing	CRONKLEY		WIDDYBANK	
	Small	Medium	Small	Medium
5	35	37	24	24
10	58	55	54	53
Final per cent germination	96.66	91.66	90.00	88.33
Total per cent germination : 92.92				

There is no difference in the speed or success of germination which can be related to seed size. Cronkley seed germinated more rapidly ($X^2 = 9.20$; d.f. = 1; $0.01 > p > 0.001$), but the difference had disappeared after ten days.

Seed age and germination success

Seeds have been collected and dried - as described in section 4.1.1 - over a number of years. The seeds have been stored in the laboratory in sealed seed packets.

In spring 1976 several samples of differently-aged Draba seed were sown to assess the affect of age on germination success.

Unfortunately, no stringent observations were made to rule out the effect of seed size differences between these samples, though there was no obvious difference (Marren, pers. comm.).

The results of this experiment are expressed in figure 4.2.3.a.

At one extreme a clear indication exists of loss of viability with age, the 1972 sample having the lowest germination success. It is interesting to note that a 1973 sample (see Table 4.2.3.a) sown at the same time had a final germination success of about forty-five per cent. This is intermediate between that of the 1972 sample and those from 1974 and 1975, suggesting a progressive loss of viability with age.

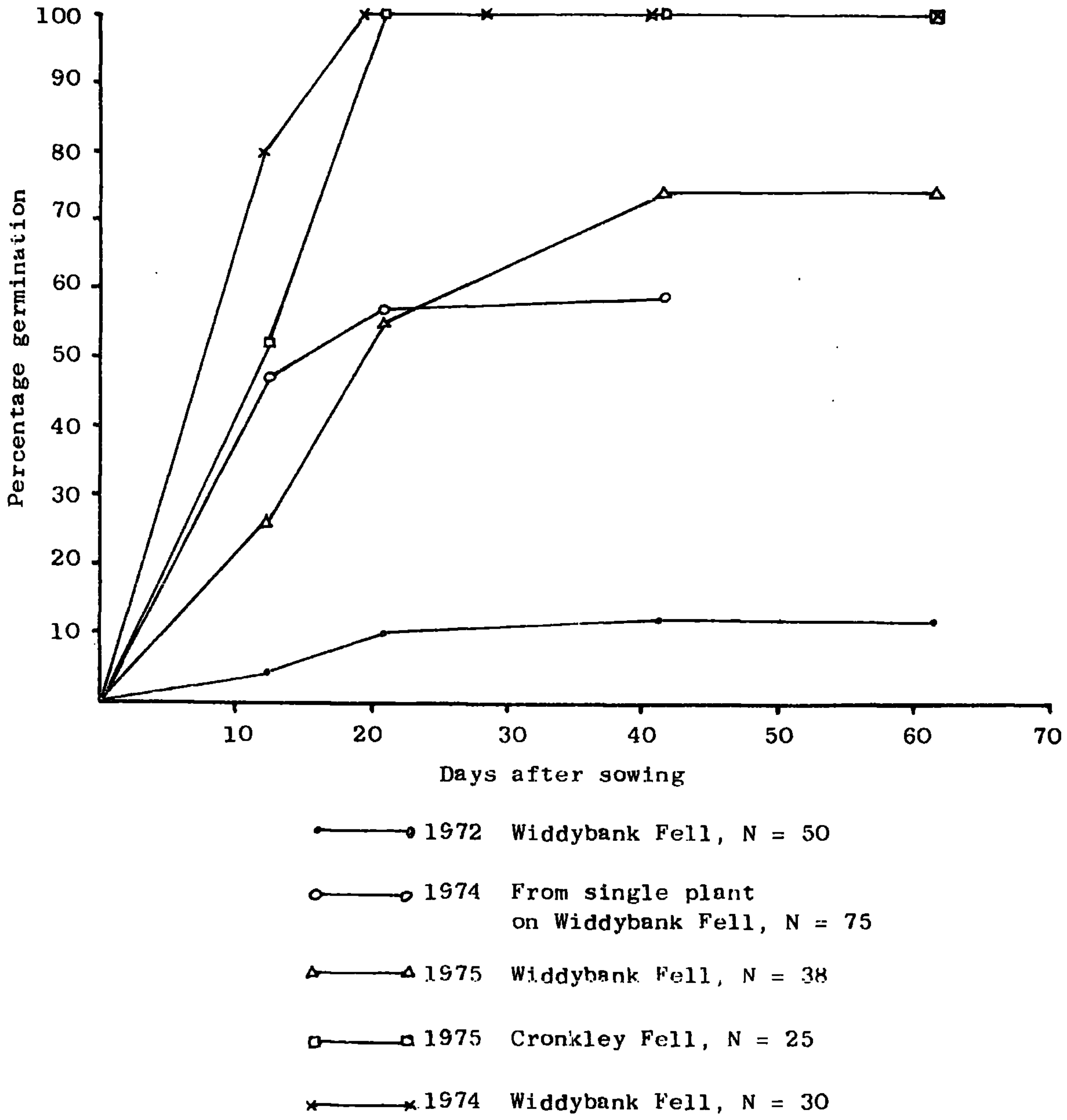


Figure 4.2.3.a : Seed germination related to age (after Marren, unpubl.)

Substrate and germination success

This experiment was carried out in 1969 (Muggleton, unpubl.). Seed samples were potted out in John Innes Seedling Soil and in sugar-limestone soil. The pots were placed in a greenhouse.

As can be seen in figure 4.2.3.b, rapid germination to almost one hundred per cent occurred on sugar-limestone soil after a delay. In contrast, germination on compost occurred much less abruptly, achieving a lower final percentage.

Actual figures are not available for this experiment, sample sizes are unknown.

B. Fell-top

In 1969 five sites were selected on Widdybank fell to assess the success of germination and subsequent establishment.

Seeds were scattered over the surface of small pots filled to within half an inch of the rim with John Innes Seedling Soil. Each sample contained fifty seeds. These were placed in a cold frame on the fell-top and at five other separate sites on the fell.

Two control samples were maintained in the greenhouse in Durham. Both had one-hundred per cent germination.

The sample in the cold frame had eighty-four per cent germination after 120 days. No further seeds germinated after this time.

The results of those samples at the five separate sites over the fell are given in Table 4.2.3.c.

Thus, germination success decreases with the severity of the environment to which the seeds are exposed. Temperature is presumably the limiting factor here. It is instructive to compare the maximum numbers of seeds germinating at the north- and south-facing sites. Since the sites were visited infrequently, these totals probably represent an under-estimate of the numbers of seed germinating (seed may germinate and disappear between

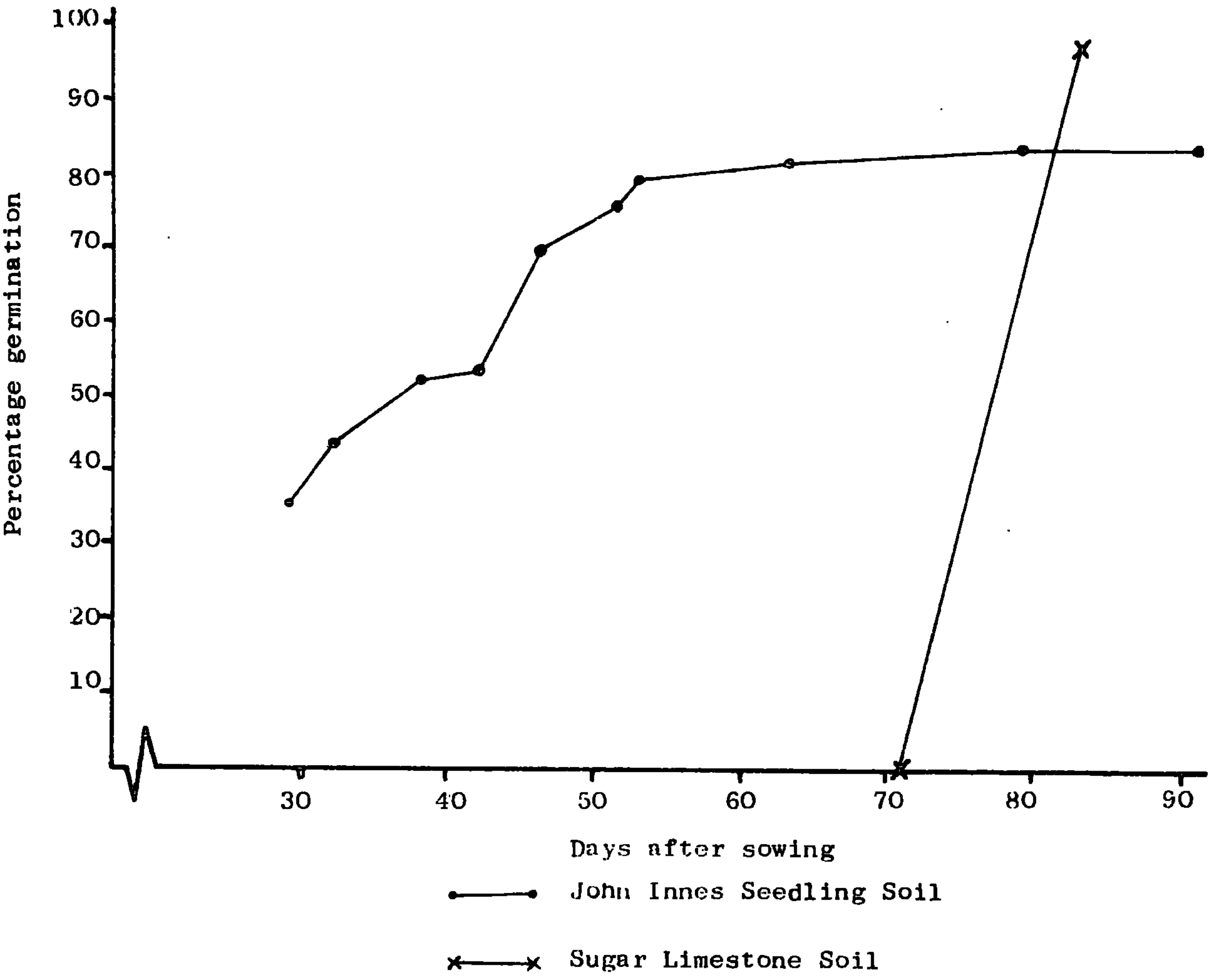


Figure 4.2.3.b : Pattern of germination related to substrate (after Muggleton, unpubl.).

Table 4.2.3.c : Fell-top germination trials (after Muggleton, unpublished).

Site	No. seeds grown	Date and Number Germinating & surviving thereafter			
		8/V	21/V	30/V	26/VI
North-facing I	50	0	4	5	1
North-facing II	50	2	2	6	0
South-facing I	50	17	9	9	2
South-facing II	50	1	41	31	0
Fell-top	50	5	5	5	5
Overall per cent germination : 29.60					

visits), though this is unlikely to affect comparisons between the two sites, which are equally likely to have seedlings missed in this way. Accepting that supposition, a clear relationship between aspect and germination success is demonstrable ($X^2 = 67.9778$; d.f. = 1; $0.001 \gg p$).

A further set of fell-top germination experiments were carried out using seed collected in 1976. These were sown directly on to the soil-surface in what, to a visual examination, appeared to be suitable Draba sites.

A mixture of thirty seeds and a small amount of baked sand (to facilitate scattering of seed) was sown inside two "mini-quadrats" of 9 cm^2 and 25 cm^2 respectively. Each density was replicated three times at each of three sites on the fell; one lowland (Durham) site; and one in the laboratory, as in the first paragraph of this section.

The aim was to assess the effect of density on seedlings on subsequent survival. Unfortunately, no germination took place on the fell.

The laboratory control (also at two densities, three replicates) produced an overall germination figure of eighty-five per cent. This is significantly lower than those sown directly on to filter-paper ($X^2 = 5.2915$; d.f. = 1; $0.05 > p > 0.02$).

Possible interactions between seed size, density, substrate and germination success are taken up in the discussion.

4.3 Establishment

This section deals with the behaviour of the youngest plants on the fell: newly germinated seedlings of Polygala and Draba, ramets of gentian. For reasons discussed in the previous section, seedlings are likely to grow from seed set in the previous year. Ramets of gentian arise from underground stolons produced by established plants. It is not known at what stage these become independent of the parent plant. Connections are impossible to detect in the field without uprooting the plants. Appearance of new individuals of either sort is taken to constitute an addition (recruit) to the population.

The mortality of this earliest stage in the life-history has been analysed over the first growing season on the fell, i.e. a period of up to nine months, ending after the autumn recording in the year of recruitment.

Data available for the three species differs and so, therefore, does the presentation. This is a reflection of the differing strategies of the three species. An outline of this, as it is relevant to the results, follows.

A. Draba incana

The small, light seeds are dispersed widely by wind. Often, the valves are lost whilst the replum and seeds remain attached to the parent plant. Seeds are then lost over a period of time as they become detached from the replum. It has been noted that whole capsules may become detached. (Bradshaw, pers. comm.) and even whole fruiting plants (Bradshaw and Doody, in press) uprooted and blown for some considerable distance, serving to disperse seed widely.

In the early years of the study several dense clusters of seedlings were recorded in the permanent plots, as a result of germination in a restricted space of the complement of seeds from ripe capsules (Doody, pers. comm.). These clusters were seen on the fell at a density of around 20 cm^{-2} in 1977. The data available reflect the chance interaction of viable seed with a suitable germination site. They are available only from the years 1970 to 1973, no large numbers of seedlings having germinated in the permanent plots recently. These groups of seedlings were counted at short intervals and survivorship curves have been drawn (see figure 4.3.a). Figures over six-monthly periods have been abstracted from these to provide a comparison with Gentiana and Polygala.

B. Polygala amarella

Seeds remain inside the capsules when the latter drop from the parent plant. They invariably fall close to the parent, fragments of capsules remaining visible in the plots throughout the growing season after that in which they ripened. Information has not been collected on seedling decay at short intervals. Results are presented as a mortality rate over approximately six-monthly periods.

C. Gentiana verna

The seasonal pattern of appearance of ramets of the gentian is similar to that of seedlings of Polygala. They have been seen to appear at distances up to 25 cm from the nearest plant in cultivation on sugar-limestone soil in Durham (Gibbons, pers. comm.). Results are presented in a similar way to Polygala.

Since the latter two species produce smaller numbers of recruits, data from all the permanent plots have been pooled to give as large a sample as possible. This is unnecessary for Draba since large numbers are involved.

Mortality in the first six months

The results are displayed in figure 4.3.a and Table 4.3.a.

No consistent differences between the first and second three-month

Table 4.3.a : Comparison of mortality over first and second three-month periods: *Polygala amarella* and *Gentiana verna*, Widdybank Fell populations

Year	*Polygala amarella*					*Gentiana verna*				
		Survivors		Mortality			Survivors		Mortality	
	Spring Recruits	to Summer	to Autumn	First three months	Second three months	Spring Recruits	to Summer	to Autumn	First three months	Second three months
1969	0	0	0	-	-	-	-	-	-	-
1970	11	8	6	0.2727	0.2500	79	73	70	0.0759	0.0411
1971	19	19	18	0.0000	0.0526	75	70	58	0.0667	0.1714
1972	29	29	27	0.0000	0.0690	30	30	27	0.0000	0.1000
1973	0	0	0	-	-	12	11	10	0.0933	0.0909
1974	16	16	16	0.0000	0.0000	18	17	16	0.0556	0.0588
1975	6	6	6	0.0000	0.0000	34	34	33	0.0000	0.0294
1976	12	5	5	0.5833	0.0000	67	60	56	0.1045	0.0667
Totals	93	83	78	0.1075	0.0602	315	295	270	0.0635	0.0847

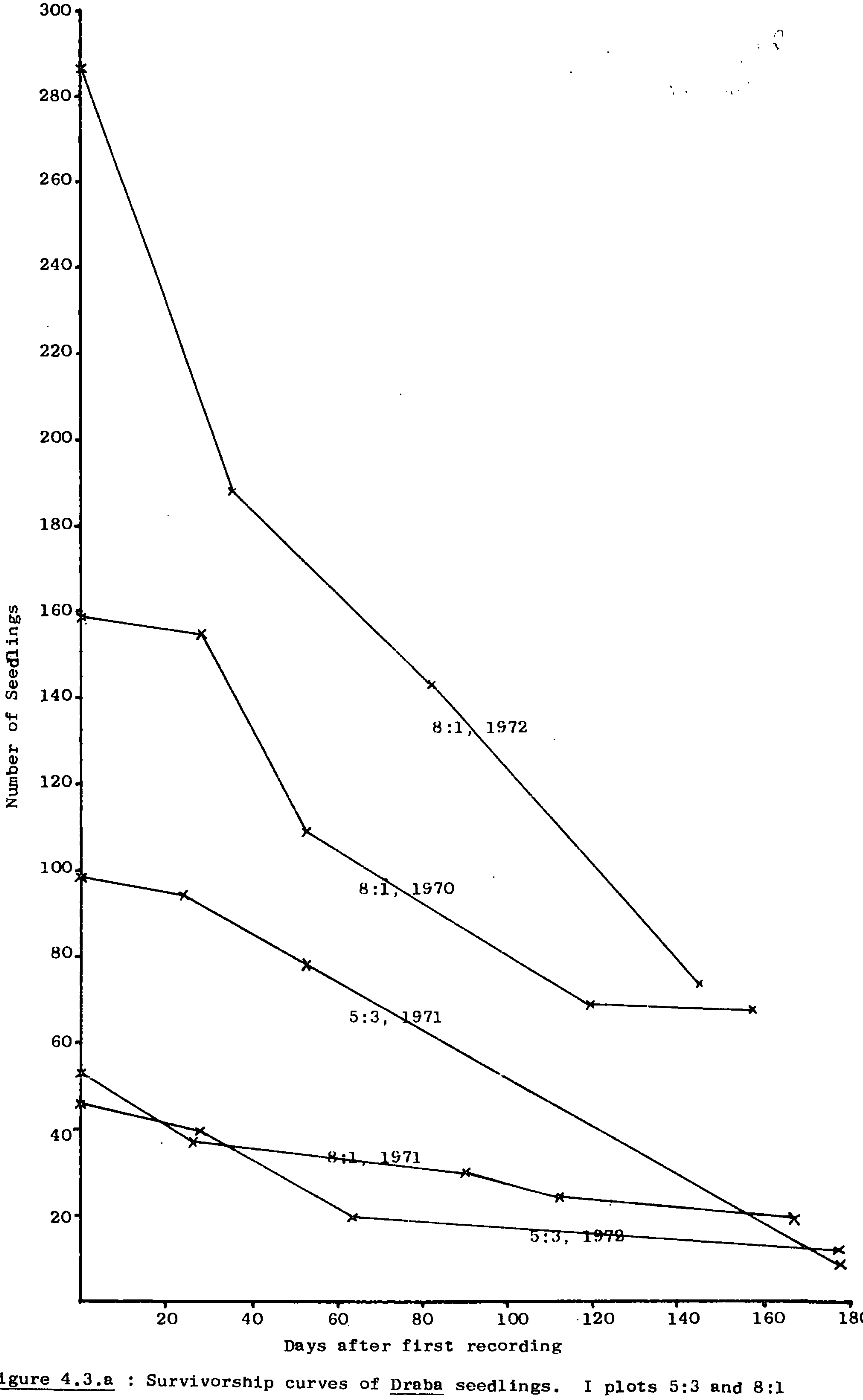


Figure 4.3.a : Survivorship curves of Draba seedlings. I plots 5:3 and 8:1

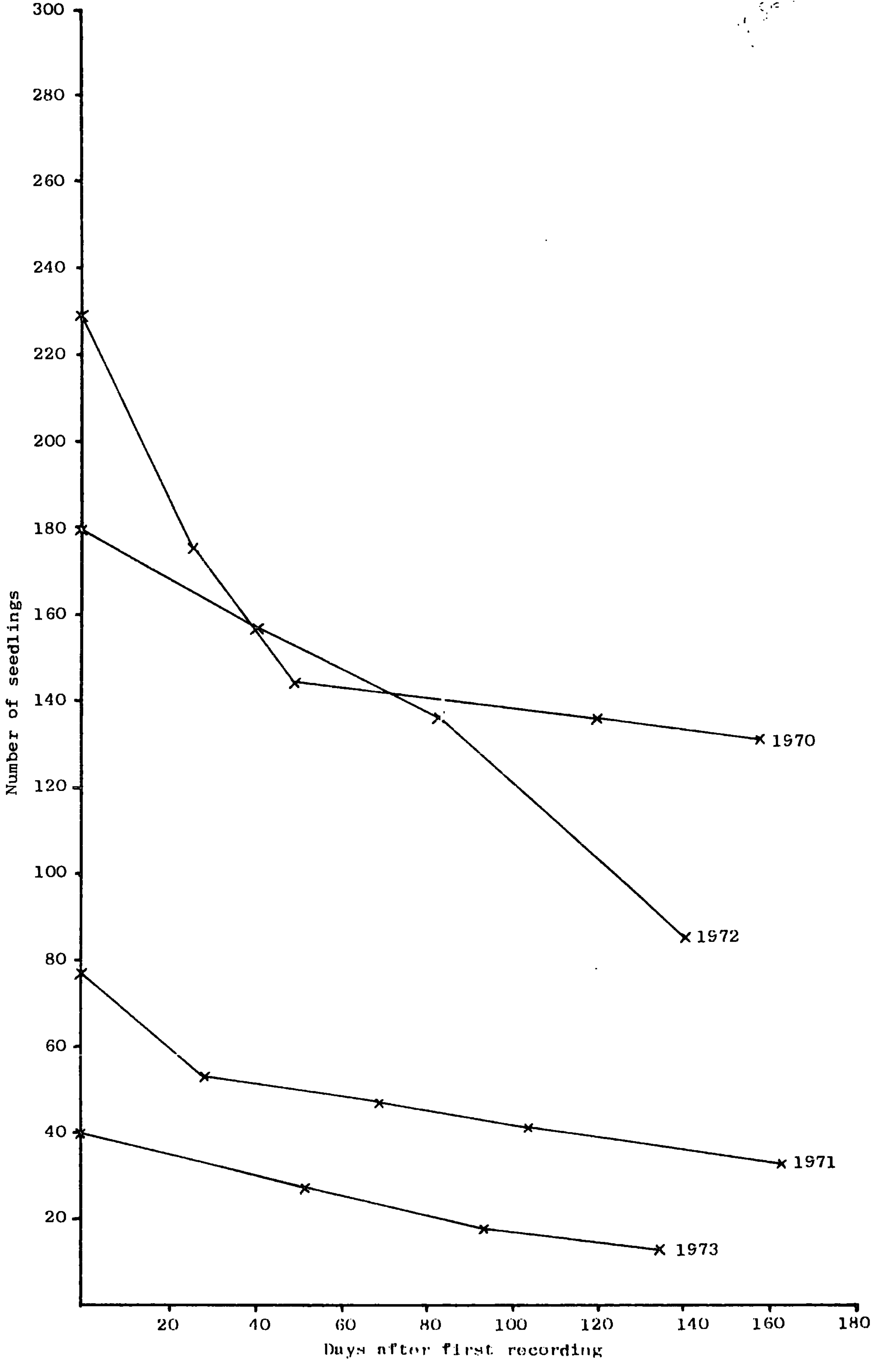


Figure 4.3.a (cont.) : Survivorship curves of *Draba* seedlings. II plot 2:1.

periods are demonstrable in either Polygala or Gentiana over the whole of the study period. The overall totals, therefore, represent the behaviour of these plants adequately. In both species, there is no change in mortality over the first six months.

This conclusion stands in marked contrast to the behaviour of Draba seedlings. In six out of the nine survivorship curves displayed in figure 4.3.a, the steepest part of the curve, corresponding to the highest mortality rate comes in the first two months after germination. One should point out here that, since seedlings may germinate and die between recordings, these figures may underestimate seedling mortality. Mortality of new individuals of Polygala and gentian is probably not underestimated in this way, since even at their youngest, recruits may be identified individually. This is due to their larger size and lack of dense clumping.

There is some indication from figure 4.3.a that mortality of Draba seedlings is greater when initial numbers are high, curves with a greater starting number appearing steeper overall. No information is available to relate mortality to density changes, however, due to the way in which Draba seedlings germinate. One would assume an intra-specific density-dependent mechanism operates on this species when it germinates in great numbers.

Both Polygala and Gentiana show their highest early mortality in the summer of 1976. This was undoubtedly due to the drought experienced in that year, which affected all species at all sites under examination. High mortalities were recorded over the fell generally at that time (see later sections).

Mortality over the first year

Overall, the mortality of young gentian rosettes is greater than that of Polygala, the greatest difference occurring during the over-winter period. Polygala maintains a constant mortality rate per plant of about 0.16 throughout this period. On a between-year basis, these trends are by

Table 4.3.b : Comparison of mortality over first and second six-month periods: <u>Draba incana</u>, <u>Polygala amarella</u> and <u>Gentiana verna</u>, Widdybank Fell populations

Year	Polygala amarella					Draba incana					Gentiana verna				
	Survivors			Mortality		Survivors			Mortality		Survivors			Mortality	
	Spring recruits	To autumn	To following spring	First six months	Second six months	Spring recruits	To autumn	To following spring	First six months	Second six months	Spring recruits	To autumn	To following spring	First six months	Second six months
1969	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-
1970	11	6	6	0.4545	0.0000	388	199	180	0.4871	0.0955	79	70	61	0.1139	0.1286
1971	19	18	12	0.0526	0.3333	227	63	29	0.7225	0.5397	75	58	52	0.2267	0.1034
1972	29	27	25	0.0690	0.0741	413	173	94	0.5811	0.4566	30	27	26	0.1000	0.0370
1973	0	0	0	-	-	40	13	10	0.6750	0.2308	12	10	9	0.1667	0.1000
1974	16	16	13	0.0000	0.1875	-	-	-	-	-	18	16	15	0.1111	0.0625
1975	6	6	5	0.0000	0.1667	-	-	-	-	-	34	33	19	0.0294	0.0424
1976	12	5	4	0.5833	0.2000	-	-	-	-	-	67	56	33	0.1642	0.4107
Totals	93	78	65	0.1613	0.1667	1,068	448	313	0.5805	0.3013	366	293	215	0.1995	0.2662

no means as clear-cut, so while the overall behaviour of young plants is as stated, fluctuations and variations due to seasonal effects are the most obvious feature of the data when viewed as a whole. Once again, 1976 stands out as a year with high mortality.

Mortality of Draba plants is clearly concentrated in the first six months of life. For each of the four years from which data are available this pattern is repeated.

5. RECRUITMENT

5.1 Recruitment Rates

This section is concerned with the numbers of new individuals entering the population.

Since neither Polygala nor Gentiana has significantly higher mortality in the establishment phase, all seedlings and ramets respectively have been summed for each species within a particular year to calculate the rate of recruitment for that year. Draba, having high early mortality risk, is treated in a different way: only seedlings surviving until autumn of their year of appearance are included. It would clearly be misleading to use the totals of all Draba seedlings in this calculation since most are so short-lived.

Results are summarized in Table 5.1.a.

Mean recruitment rates, while quantifying the overall situation in the populations over the whole of the study period, should be treated with some caution. The very high chi-squared values confirm a very heterogeneous set of data in each case. Chi-squared values for individual years enable the sources of the overall heterogeneity to be identified.

The two Polygala populations show a broad overall synchronization. The single greatest and two least annual deviations from the mean recruitment rate occur in the same years.

Recruitment in Draba incana is the most variable of the three. Only one yearly recruitment rate corresponds to the overall value.

Gentian shows an overall level of heterogeneity in the data similar to Polygala.

Recruitment was highest in both Polygala populations in 1969. The Widdybank population maintained fairly high recruitment in 1970. This observation should, however, be treated with some caution since the Cronkley

Table 5.1.a : Recruitment rates in the four populations over the study period

	Polygala amarella								*Draba incana*				*Gentiana verna*			
	CRONKLEY				WIDDYBANK				WIDDYBANK				WIDDYBANK			
Year	Spring total	Total seedlings	Recruitment rate	Chi-squared	Spring total	Total seedlings	Recruitment rate	Chi-squared	Spring total	Seedlings*	Recruitment rate	Chi-squared	Spring total	Total Ramets	Recruitment rate	Chi-squared
1969	73	118	1.6164	73.07	104	137	1.3173	61.87	152	117	0.7697	9.78	293	107	0.3652	0.76
1970	131	26	0.1985	2.00	145	78	0.5380	4.82	180	224	1.2444	63.43	251	224	0.8924	42.65
1970	116	14	0.1207	5.54	183	39	0.2131	4.30	331	63	0.1903	31.44	356	140	0.3933	0.18
1972	89	19	0.2135	1.00	167	50	0.2994	9.72	248	174	0.7016	9.72	361	106	0.2936	5.85
1973	85	11	0.1294	3.66	164	16	0.0976	14.31	263	30	0.1141	42.62	357	91	0.2549	10.36
1974	80	4	0.0500	7.74	139	23	0.1655	6.14	220	19	0.0864	42.32	347	90	0.2593	9.48
1975	83	11	0.1325	3.44	121	15	0.1240	8.28	+99	55	0.5556	0.50	315	108	0.3429	1.74
1976	35	10	0.2857	0.02	68	26	0.3824	0.07	71	68	0.9577	11.21	226	175	0.7743	23.19
Totals	692	213	0.3078	96.47	1,091	384	0.3520	100.32	1,564	750	0.4795	211.02	2,506	1,041	0.4154	94.21
Means	86.5	26.6		$p \ll 0.001$	136.4	48		$p \ll 0.001$	195.5	93.8		$p \ll 0.001$	313.3	130.1		$p \ll 0.001$

* only those surviving to autumn in year of recruitment.

\+ autumn total - spring total not available.

population almost doubled between 1969 and 1970, while the Widdybank Fell population increased by less than half. Greater continued recruitment in 1970 may thus have been possible on Widdybank Fell only because of relatively poor establishment in the previous year.

Both Draba and gentian had high recruitment in years 1970 and 1976. One may not conclude that they are favoured by similar conditions, however, since actual number of recruits of each (relative to their overall means) are quite different: that for Draba being lower, and gentian higher.

5.2 Seasonal Pattern of Recruitment

As has been discussed earlier, Draba germinates in spring and new recruits have not been counted until autumn in most years. Analogous data to those for Polygala and gentian are not, therefore, available.

Results for both populations of Polygala and that of Gentiana are displayed in figure 5.2.a.

The spring total for each species theoretically includes all those plants appearing after the last (i.e. autumn) recording of the previous year. Doody[21] records that most Polygala seeds germinate in the year after seed set. This being the case, the histograms probably represent an accurate picture of the annual pattern of germination of seed which has overwintered on the fell. Small numbers of those in the autumn totals may be from seed set in the same year. Both populations show significantly different recruitment in the three seasons.

The behaviour of the gentian population is quite different. Recruitment is a fairly continuous process throughout the year (being a vegetative process, it is not restricted by such factors as flowering period and enforced seed dormancy), no significant difference between seasons being demonstrable. It should be noted that there is a six-month gap between the autumn recording of one year, and the spring recording of the next. A gap of only three months occurs between spring and summer, and summer

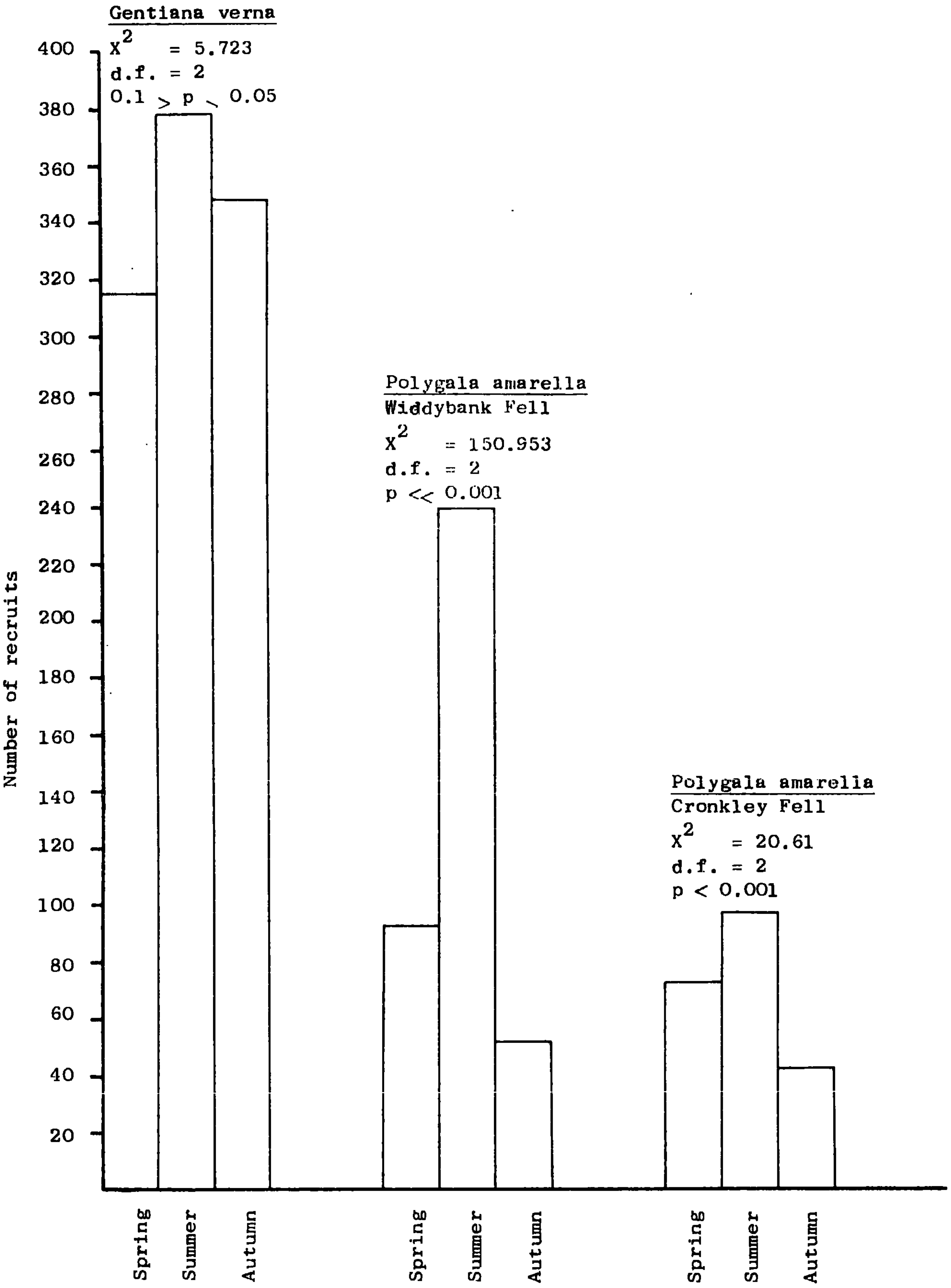


Figure 5.2.a : Seasonal pattern of recruitment.

and autumn records. If recruitment continued throughout the year at the same rate, a high spring total would be expected. This is not the case. If the number of spring recruits is halved - to allow for the longer time interval - and the data are then tested for heterogeneity, a significant result is obtained ($X^2 = 97.13$; d.f. = 2; $p \ll 0.001$). Recruitment is thus lower in the winter, a result of depressed metabolism in the cooler months.

6. MORTALITY

Tables 6.a, I-IV summarize mortality in the four study populations. The total number present in the mixed-age population at the beginning of the study period and of recruits added in successive years are entered at autumn in the year of recruitment (early mortality is dealt with in section 4.3). Thereafter the total number surviving is given at six-monthly intervals: the autumn and spring records. Mortality rates summarize the behaviour of the population in two ways.

(a) Horizontal

Annual and six-monthly mortality rates have been calculated, giving an indication of adverse years and a seasonal rhythm in the mortality of the plants.

(b) Diagonal

Plants of the same age across successive cohorts have been lumped and a mortality rate calculated over successive periods, giving an indication of any age-specificity in the overall pattern of mortality.

The age classes differ between species. Polygala amarella and Gentiana verna are analogous since recruits are recorded at all three seasons for both species. The first entry for any cohort represents plants surviving to autumn from recruits first seen in spring, summer and autumn of that year. Since both these species have the potential to recruit in all three seasons, certain of the plants entered at the head of each cohort may be up to one year old. A spread of ages is thus represented in each cohort.

The same is not true for Draba incana where plants are up to six months old when they are lumped into annual cohorts. The spread of ages within a cohort is consequently less.

These differences are due to the seasonal pattern of recruitment

Table 6.a.I : Mortality. *Draba incana*, Widdybank Fell

Year	Season	Mixed-age pop.	Cohorts						
1969	Spr	152							
1969	Aut	82	117						
1970	Spr	71	109						
1970	Aut	49	93	224					
1971	Spr	42	86	203					
1971	Aut	28	62	185	63				
1972	Spr	23	54	142	29				
1972	Aut	20	45	112	22	174			
1973	Spr	18	41	87	22	95			
1973	Aut	18	40	86	22	90	30		
1974	Spr	9	32	69	19	65	26		
1974	Aut	9	24	66	19	58	26	19	
1975	Spr	7	-	-	-	-	-	9	
1975	Aut	5	16	25	6	27	11	9	55
1976	Spr	2	5	8	2	4	3	3	44
1976	Aut	1	0	2	1	2	3	1	44

Age-specific* Mortality rates : (Oldest) 1.0000 0.6327 0.5536 0.3559 0.3208 0.3741 0.3123 (Youngest).

MORTALITY RATE (per Plant)	
Annual	Six-Monthly
	0.4605(S-A)
0.2864('69-'70)	0.0955(A-S)
	0.2111(S-A)
0.2486('70-'71)	0.0956(A-S)
	0.1692(S-A)
0.4112('71-'72)	0.2663(A-S)
	0.1976(S-A)
0.2332('72-'73)	0.2949(A-S)
	0.0266(S-A)
0.2937('73-'74)	0.2308(A-S)
	0.0818(S-A)
0.5220('74-'75)	0.4286(A-S)
	0.1250(S-A)
0.6494('75-'76)	0.5390(A-S)
	0.2394(S-A)

* ages explained in text.

Table 6.a.II : Mortality. *Gentiana verna*, Widdybank Fell

Year	Season	Mix-Age pop.	Cohorts							MORTALITY RATES (Per Plant)	
										Annual	Six-Monthly
1969	Spr	293									
1969	Aut	-	104								
1970	Spr	169	82							0.3173('69-'70)	0.2115(A-S)
1970	Aut	138	71	208							0.1673(S-A)
1971	Spr	117	59	180						0.2973('70-'71)	0.2974(A-S)
1971	Aut	91	51	151	118						0.1770(S-A)
1972	Spr	85	44	127	105					0.2628('71-'72)	0.1217(A-S)
1972	Aut	66	34	107	96	101					0.1607(S-A)
1973	Spr	57	34	98	78	90				0.2129('72-'73)	0.1163(A-S)
1973	Aut	51	27	86	73	81	89				0.1092(S-A)
1974	Spr	44	23	78	61	71	70			0.2948('73-'74)	0.1474(A-S)
1974	Aut	36	20	68	52	54	57	88			0.1729(S-A)
1975	Spr	28	17	53	44	45	47	81		0.2800('74-'75)	0.1600(A-S)
1975	Aut	27	17	50	38	39	34	65	106		0.1429(S-A)
1976	Spr	15	8	32	27	25	22	38	59	0.4574('75-'76)	0.3938(A-S)
1976	Aut	10	4	25	22	22	15	26	48		0.2389(S-A)
Age-Specific* Mortality rates		: (Oldest)	0.7647	0.4000	0.3083	0.2654	0.2915	0.3378	0.3010	(Youngest)	

* ages explained in text.

Table 6.a.III : Mortality. *Polygala amarella*, Widdybank Fell

Year	Season	Mixed-age pop.	Cohorts						
1968	Aut	118							
1969	Spr	104							
1969	Aut	67	123						
1970	Spr	55	90						
1970	Aut	49	80	69					
1971	Spr	46	70	67					
1971	Aut	42	64	58	36				
1972	Spr	31	58	49	29				
1972	Aut	28	52	41	27	47			
1973	Spr	23	48	34	22	37			
1973	Aut	22	48	34	22	37	16		
1974	Spr	19	36	27	20	23	14		
1974	Aut	15	33	27	19	22	14	23	
1975	Spr	12	28	19	17	16	9	20	
1975	Aut	12	26	17	16	14	8	20	15
1976	Spr	8	10	11	9	5	5	9	11
1976	Aut	6	8	5	4	2	1	5	7

Age-specific* Mortality Rates : (Oldest) 0.6923 0.3800 0.4066 0.2185 0.2357 0.3136 0.2614 (Youngest)

MORTALITY RATES (Per Plant)	
Annual	Six-Monthly
0.4322('68-'69)	0.1186(A-S) 0.3558(S-A)
0.3211('69-'70)	0.4380(A-S) 0.1103(S-A)
0.1717('70-'71)	0.0758(A-S) 0.1038(S-A)
0.2600('71-'72)	0.1650(A-S) 0.1138(S-A)
0.1641('72-'73)	0.1590(A-S) 0.0061(S-A)
0.2737('73-'74)	0.2235(A-S) 0.0647(S-A)
0.2614('74-'75)	0.2092(A-S) 0.0661(S-A)
0.7031('75-'76)	0.4687(A-S) 0.4411(S-A)

* ages explained in text.

Table 6.a.IV : Mortality. *Polygala amarella*, Cronkley Fell

Year	Season	Mixed-age pop.	Cohorts						
1968	Aut	96							
1969	Spr	73							
1969	Aut	55	109						
1970	Spr	39	92						
1970	Aut	35	81	23					
1971	Spr	31	67	18					
1971	Aut	29	62	16	10				
1972	Spr	18	45	16	10				
1972	Aut	16	37	14	9	19			
1973	Spr	13	33	13	9	17			
1973	Aut	12	32	13	9	17	11		
1974	Spr	11	27	11	7	14	10		
1974	Aut	11	27	11	7	14	10	4	
1975	Spr	11	27	11	7	14	9	4	
1975	Aut	11	26	10	7	13	9	4	11
1976	Spr	6	7	1	4	7	5	1	4
1976	Aut	6	7	1	4	7	5	1	4

Age-Specific* Mortality Rates : (Oldest) 0.7308 0.2703 0.1800 0.1857 0.3056 0.2044 0.2460 (Youngest)

MORTALITY RATES (Per Plant)	
Annual	Six-Monthly
0.4271('68-'69)	0.2936(A-S) 0.2466(S-A)
0.2929('69-'70)	0.2012(A-S) 0.1145(S-A)
0.2302('70-'71)	0.1655(A-S) 0.0776(S-A)
0.3504('71-'72)	0.2393(A-S) 0.1461(S-A)
0.1263('72-'73)	0.1053(A-S) 0.0235(S-A)
0.1489('73-'74)	0.1489(A-S) 0.0000(S-A)
0.0476('74-'75)	0.0119(A-S) 0.0361(S-A)
0.6154('75-'76)	0.6154(A-S) 0.0000(S-A)

* ages explained in text.

characteristic of each species (see section 5.2).

6.1 Annual Mortality

Overall mortality rates are given below.

Species	Annual Mortality Rate (per plant)
Draba incana	0.3375
Gentiana verna	0.2775
Polygala amarella (Widdybank)	0.2692
Polygala amarella (Cronkley)	0.2319

Mortality rates, as noted above, can only form a guideline by which to judge the annual variability. Since some plants at risk in one year survive to be counted as at risk in the next, successive annual samples are not independent, and are therefore not amenable to the usual statistical tests. It is impossible to test statistically the difference between successive annual mortality rates in order to ascribe a level of significance. The problems encountered in the analysis of these data are discussed later. Here it is only possible to discuss in general terms the variability in these data, and the absence of a stringent test for comparing mortalities should be borne in mind.

These figures (above) are an average of the annual mortality rates over the study period, excluding 1975-1976 which, for all four populations, shows the highest annual rate. This was undoubtedly due to the drought of 1976 which has already been extensively documented in meteological journals[69,74,81] and its effect on chalk grassland in Sussex has been noted.[46]

Since all the populations have undergone a decline from the early part of the study period (see figures 7.2.a I-IV), the annual mortalities are calculated from progressively fewer individuals and hence more influenced by random fluctuations. The difference is not great in the case of the gentian, though it might be important in the other three populations. The high mortality rate recorded for Draba incana over 1974-1975 is illustrative of this. It is calculated from very few plants and the resulting mortality rate is the second greatest over the whole study period. With so few plants contributing to this figure it is clearly of dubious significance.

The overall annual mortality rate for Draba gives a poor representation of the mortality over the study period. Excluding 1976, it overestimates mortality in four years and underestimates it in two.

Gentiana verna showed a much more regular annual mortality over the study period and consequently the overall figure is more representative.

The Cronkley Fell population of Polygala amarella had the greatest range in mortality values. Both this and the Widdybank Fell population show the greatest variability in annual mortality out of the four populations under consideration. The direction, if not the magnitude, of change between the mortality rates of successive years shows great consistency between these two populations. This suggests that a climatic factor has some influence on mortality in this species.

6.2 Six-monthly mortality

The existence of a seasonal rhythm in mortality has now been widely demonstrated,[6,40,87] and Harper[36] considers this likely to be a widespread phenomenon, emphasising that mortality is greatest when plants are growing most rapidly.

The mortality rates were calculated over the six-month periods to give some indication if this were the case in the study populations. Results are summarized below. Overall figures for mortality here are open to the same criticisms and limitations as the annual figures.

Species	Season	Overall Mortality Rate* (per plant)
<u>Draba incana</u>	winter	0.2358
<u>Draba incana</u>	summer	0.1816
<u>Gentiana verna</u>	winter	0.1757
<u>Gentiana verna</u>	summer	0.1550
<u>Polygala amarella</u> (Widdybank)	winter	0.1984
<u>Polygala amarella</u> (Widdybank)	summer	0.1172
<u>Polygala amarella</u> (Cronkley)	winter	0.1588
<u>Polygala amarella</u> (Cronkley	summer	0.0921

* Values for 1976 have not been included

Overall, the mortality in the four study populations was greater over the winter period. It should be emphasised that the work which has demonstrated a seasonal rhythm (q.v.) was carried out over a shorter period than the present study and with more frequent recordings throughout the year. Comparisons are, therefore, only tentative.

<u>Polygala</u> demonstrates high winter mortality in six out of eight years on Widdybank Fell and seven out of eight years on Cronkley. It occurs in <u>Draba</u> in five out of seven years and in gentian in four out of seven.

In <u>Polygala</u> therefore a high winter mortality seems to be the rule, whilst for the other two species the evidence is less conclusive.

6.3 <u>Age-Specific Mortality</u>

The calculated age-specific mortality rates (see Table 6.a) are open to the same objections as the annual mortality rates. In addition, fewer and fewer plants have been seen in the older age-groups. Hence, mortality rates for older plants are based on very few individuals. The mortality rate of the oldest age-class in each population is calculated only from plants surviving between autumn 1975 and autumn 1976, the mortality would therefore be expected to be higher than for younger age-classes.

Mortality rates of the younger age-classes are, therefore, the most reliable.

In all four populations no age-specificity is apparent in the mortality rates for the first five years. On this basis alone, age-independent mortality would be assumed.

At this point it is interesting to consider the results of this study in the light of what is known about mortality patterns in plant populations. Harper's[35] pioneering paper in plant demography, "A Darwinian approach to plant ecology", contained the results of a long term study on populations of perennial herbs published by Tamm.[95,96] Log plots of the annual survivors from Tamm's study populations gave straight-line depletion curves, indicating constant annual mortality, i.e. that mortality is independent of age.

Doody[21] used the same technique with survivorship and depletion curves of the three species of this study, along with Viola rupestris, Viola riviniana and the hybrid Viola rupestris x riviniana. He concluded that all species showed negative exponential decay (Deevey[19] Type II) and went on to calculate half-life values for all, following the method of Harper.[35]

Survivorship curves of the three species of this study are plotted on arithmetic graphs in figure 6.3.a, I-IV. While the curves are overall very similar to the expected exponential shape, differences can be seen. It was thought that these differences are obscured on a log-normal plot, and hence arithmetic plots have been used.

The problems of analysing these data statistically have been outlined before. It would be useful to be able to answer the question: "Has one

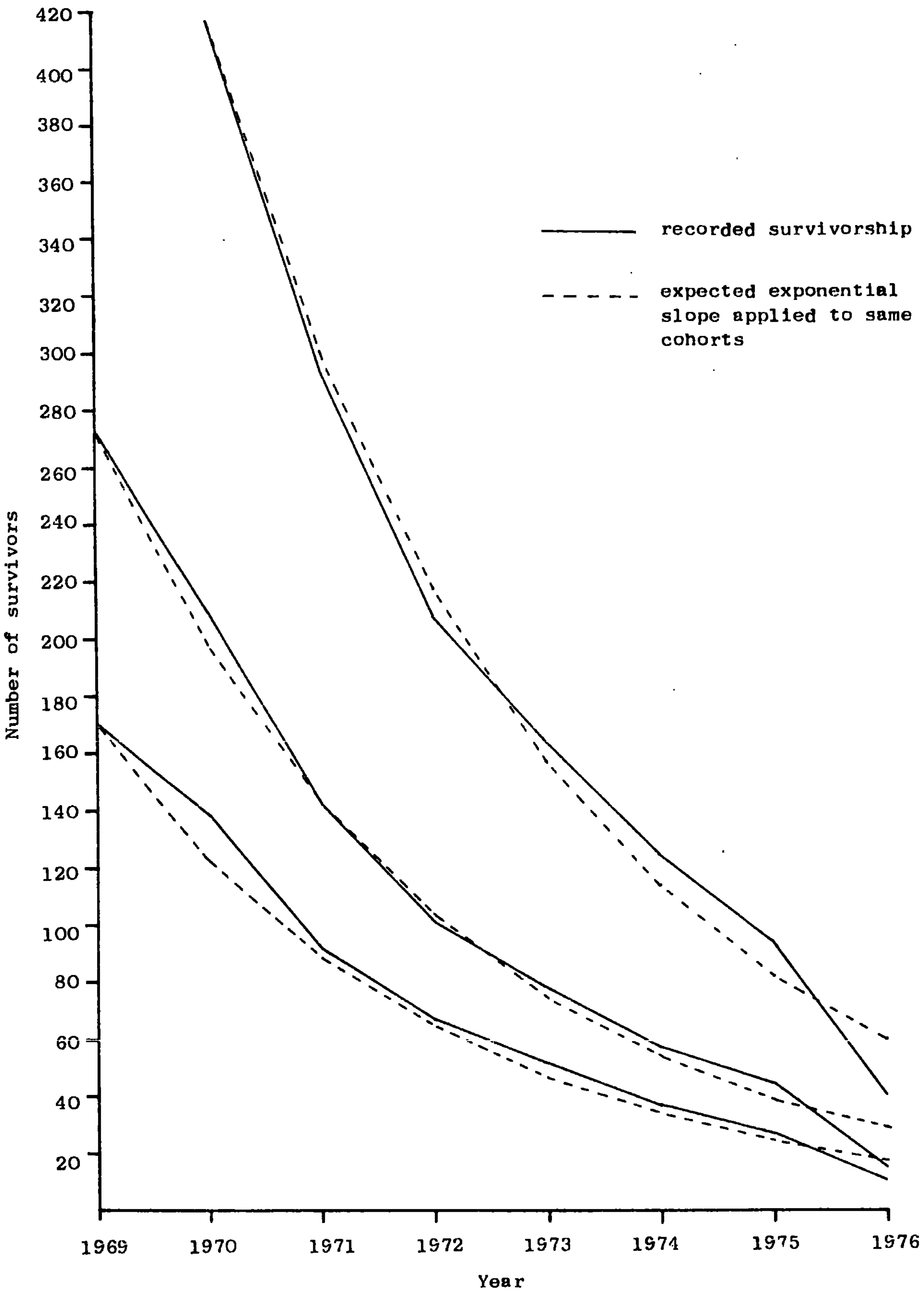


Figure 6.3.a.I : Depletion and survivorship curves of Gentiana verna.

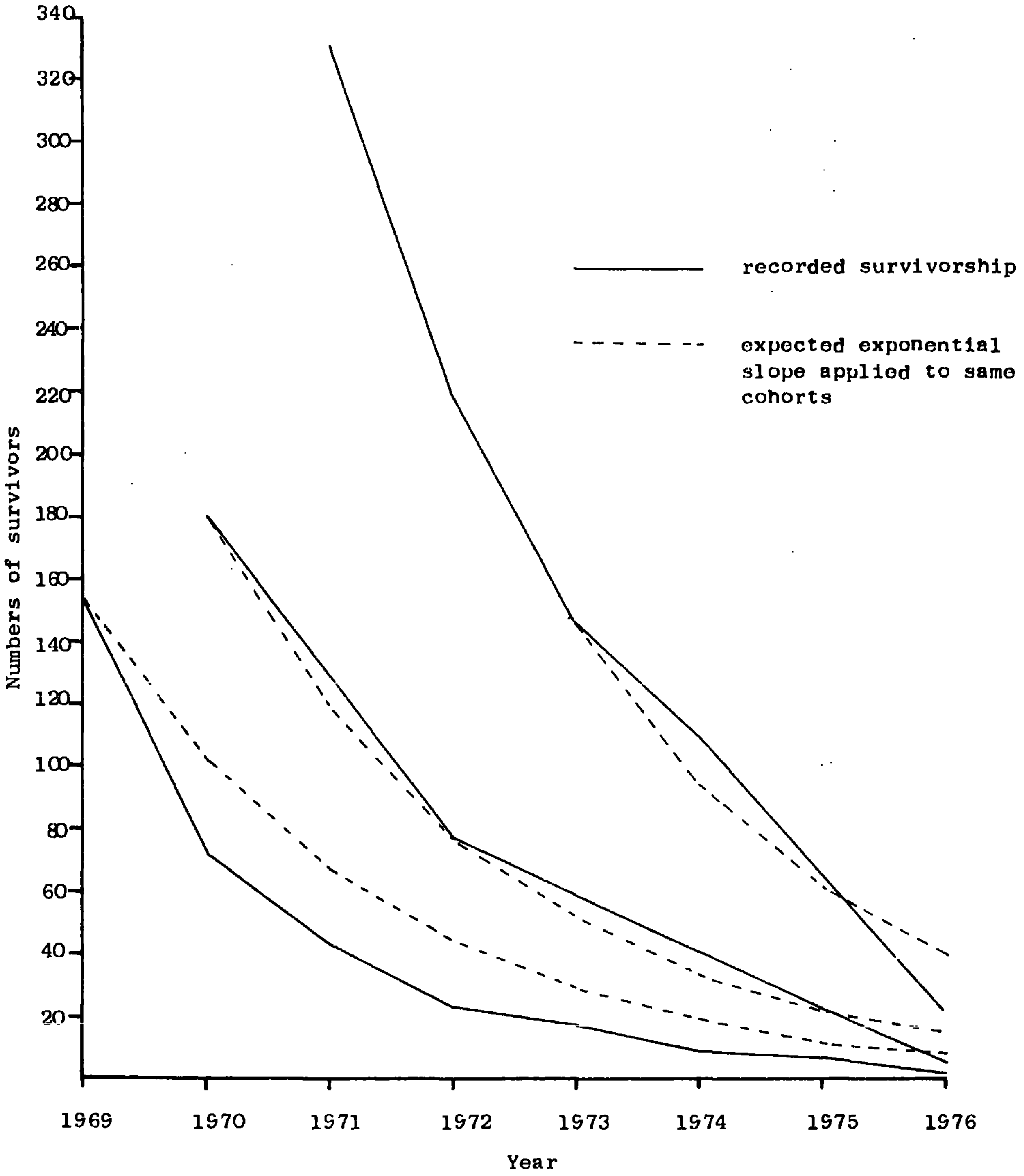


Figure 6.3.a.II : Depletion and survivorship curves of Draba incana.
(N.B. no record on survivorship curves for 1975).

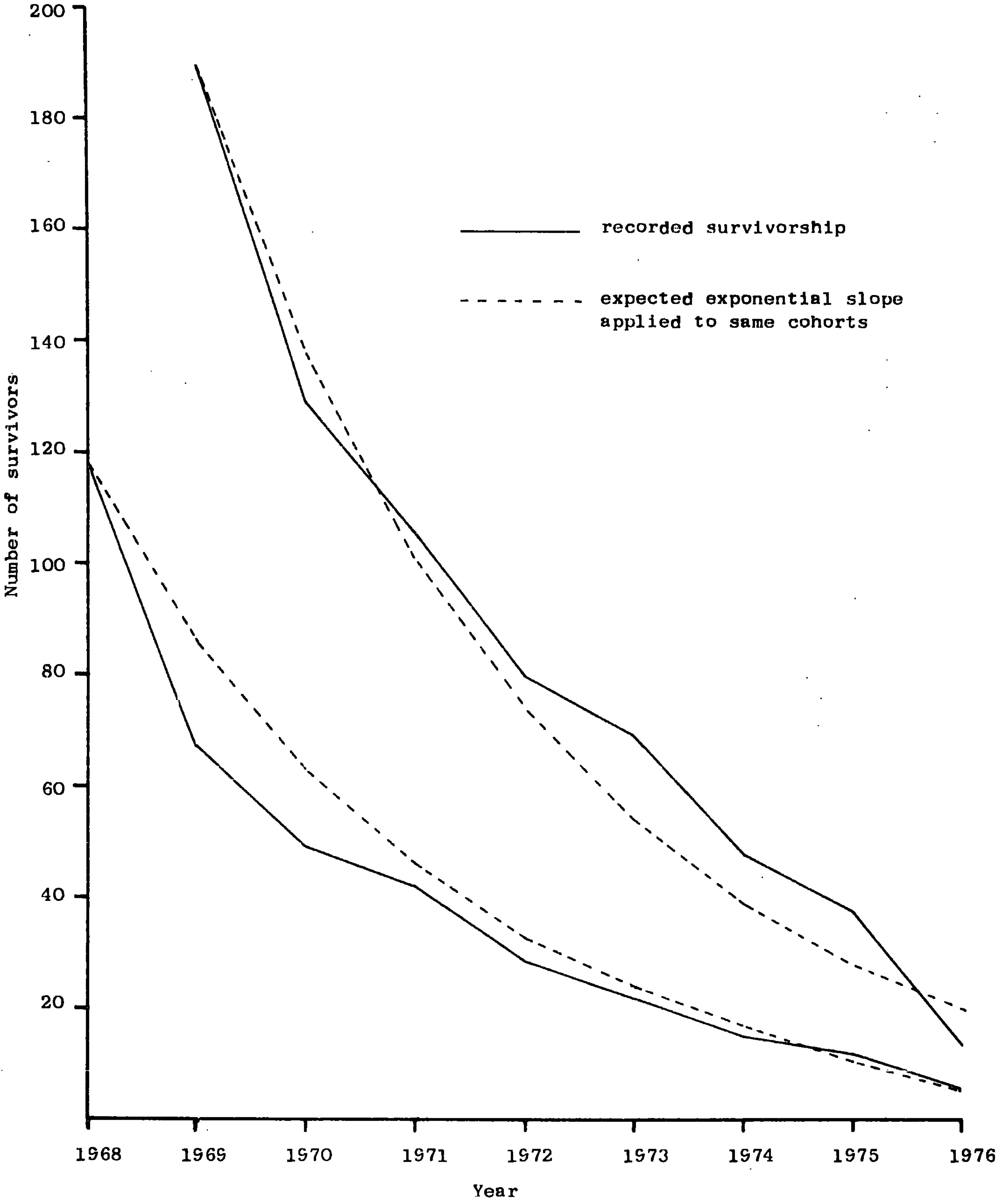


Figure 6.3.a.III : Depletion and survivorship curves of *Polygala amarella* on Widdybank.

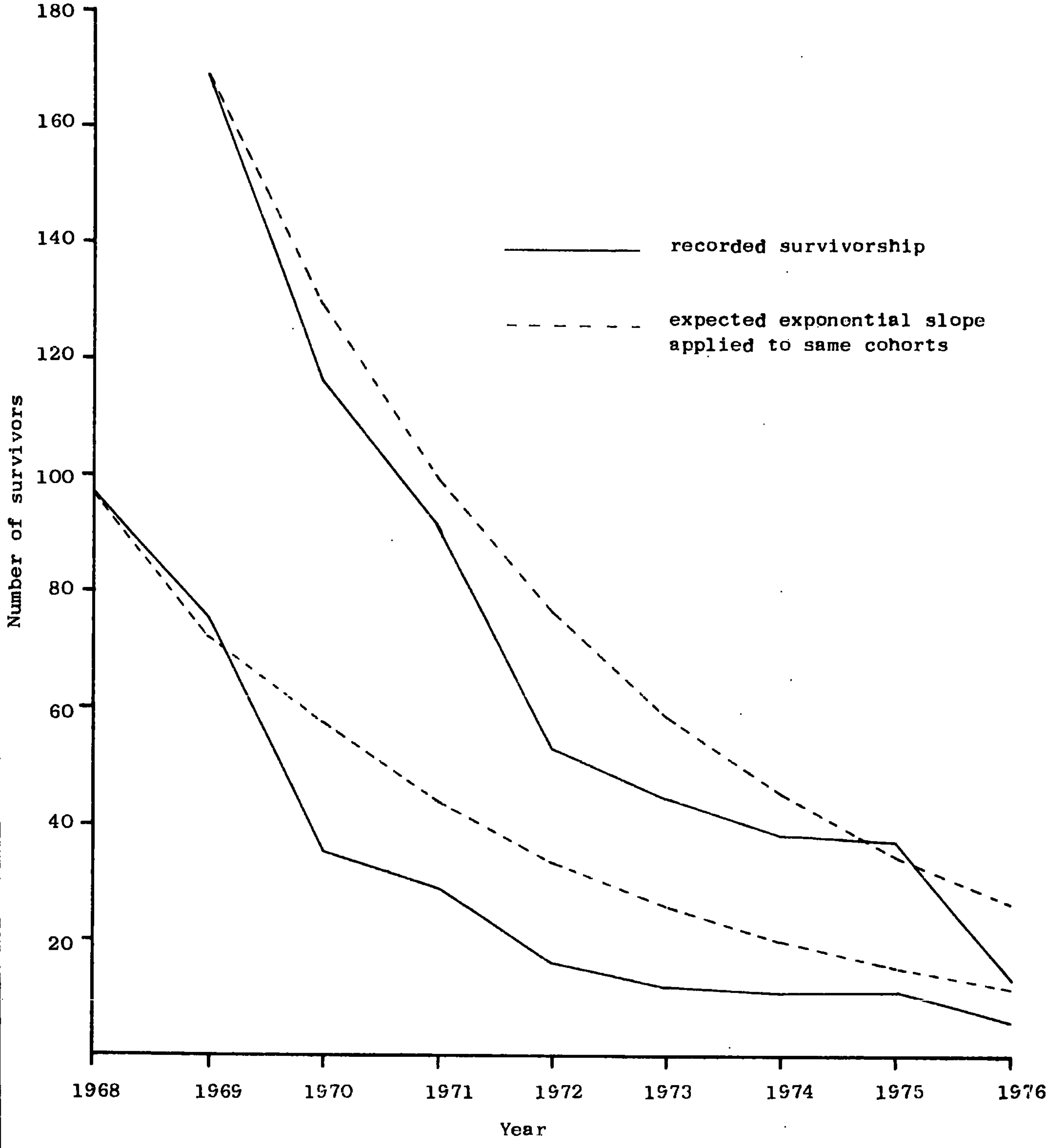


Figure 6.3.a.IV : Depletion and survivorship curves of *Polygala amarella* on Cronkley Fell.

year a significantly different mortality from the rest?" Since annual samples are not independent this is impossible using standard tests like the 't'-test. The overall shape of the curve can be compared to a theoretical exponential using the likelihood ratio test. Expected annual totals are calculated by applying a calculated overall survivorship value to the original number in the cohort. Annual observed and expected values are compared statistically. The formulae are given below.

$$(1) \quad S = \frac{\sum_{t=1}^{T-1} N_t + N_T}{\sum_{t=1}^{T-1} N_t + N_0}$$

$$(2) \quad l_h L = C + \left(l_n S\right)\left(\sum_{t=1}^{T-1} N_t + N_T\right) + \left(N_0 - N_T\right) l_n \,(1-S)$$

$$(3) \quad l_n L_{max} = C + \sum_{t=0}^{T-1} \left[N_{t+1} l_n \left(\frac{N_{t+1}}{N_t}\right) + \left(N_t - N_{t+1}\right) l_n \left(\frac{N_t - N_{t+1}}{N_t}\right) \right]$$

where S = survivorship

N = number of cohort

N_T = final number in cohort

N_0 = original number in cohort

N_t = number in cohort at time t (i.e. intermediate between N_0 and N_T

C = constant

l_n = natural log

L = likelihood

L_{max} = maximum likelihood

The final value used in the statistical test is the ratio of $l_n L$ to $l_n L_{max}$.

Explanation of Figure 6.3.a

The lowest curve in each case is the depletion curve of the original, mixed age population. Other curves are survivorship curves for the recruits added in the year at which the curve begins (to avoid confusion, the earliest cohorts only have been included on the graphs).

The expected exponential curves, drawn from the survivorship values calculated in formula (1), are given for comparison.

Curves for Gentiana verna show high correspondence between the observed and expected curves. The likelihood ratio test does not show any significant deviation from expected for any cohort over the whole of the study period. It may be concluded that, for this species, mortality is independent of age.

Results for the other three populations are summarized in Table 6.3.a.

Table 6.3.a : Results of likelihood ratio test on successive cohorts of populations of Draba incana and Polygala amarella over the study period.*

Species	Cohort begins (year)	Likelihood ratio	P-value
Draba incana (Widdybank)	1969	14.9221	+
	1970	59.7038	+++
	1971	50.7879	+++
	1972	5.6644	N/S
	1973	12.7565	+++
Polygala amarella (Widdybank)	1969	23.3609	+++
	1970	10.6501	+
Polygala amarella (Cronkley)	1969	17.1153	++

Notes: 1. * = 1976 values excluded to omit effect of the drought.

2. + = $0.05 > p > 0.01$; ++ = $0.01 > p > 0.001$; +++ = $0.001 > p$.

3. The value of the likelihood ratio is calculated in a similar manner to chi-squared. It is similarly increased by low expected values and hence certain of the cohorts, where small numbers dying, or small numbers surviving towards the end of the study period have resulted in an expected value below 5, have been omitted.

General trends

The most common pattern which emerges from the statistical analysis, and which is apparent in some of the curves plotted in figure 6.3.a, is for younger plants to survive less well than expected using an exponential model for cohort decay.

This is most obvious in the depletion curves of the two *Polygala* populations and that for *Draba incana*, along with the survivorship curves for the 1969 cohort of both *Polygala* populations (see figure 6.3.a II-IV). In each case recorded survivorship curves are steeper than expected over the first one or two years of recording after which they flatten and come to correspond more closely with the expected curve. The "tail" of the observed survivorship curve tends to be longer than expected, an effect which is somewhat obscured by the increased mortality caused by the drought in 1976.

Hett and Loucks[42] and Hett[41] have found that a power function model, implying a decreasing mortality rate with age, gave consistently higher order fit than a negative exponential model to the observed age structure and survivorship curves of balsam fir and eastern hemlock and to sugar maple seedling survivorship curves.

Unfortunately time has not allowed fitting of the data from this study to a power-function model, though this would be the obvious step to make in further analysing the present data.

While fitting a power-function model is the best means of discovering decreasing mortality with age in the observed data, indications can be gleaned from the present analysis.

All the original, mixed-age populations of Doody's[21] species: *Viola rupestris*, *Viola riviniana*, *Viola rupestris x riviniana*, *Draba incana*, *Polygala amarella* and, in addition, unpublished results on *Carex ericetorum* give significant deviation from negative exponential when tested using the likelihood ratio test. In every case, the observed number dying over the first year interval is greater than expected.

Tamm's[96] data have been tested using the likelihood ratio test. Only plants present at the beginning of his study were used, equivalent to the original, mixed-age population of this study. In all the cases tested: Sanicula europaea, plots 39 and 40; Filipendula vulgaris; Anemone hepatica and Centaurea jacea, expected values are too small (see note 3, Table 6.3.a) to enable the calculated value of the likelihood ratio to be relied upon. Composition of observed number dying against expected over the first year also produces no common trend. Hence, no difference from negative exponential is demonstrable in these data and Harper's[35] conclusions are not refuted.

Sarukhan and Harper[87] studied Ranunclulus repens, R. acris and R. bulbosus in a grazed grassland community. Their conclusions on the mortality patterns shown by the three species may be summarized as follows.

1. Depletion curves of all three species are negative exponential (Deevey type II) in form; the initial phase of rapid loss of individuals of R. acris being attributed to large numbers of newly recruited seedlings present in the mixed-age population of this species.

2. Survivorship curves of ramets are negative exponential in form from the time of appearance of the new individual.

3. Survivorship curves of seedlings are of a form indicating decreasing mortality rate with age, until they reach a certain age and the pattern of decay becomes negative exponential.

The survivorship data given by Sarukhan and Harper[87] have been analysed using the likelihood ratio test.

Numbers of plants surviving from the original mixed-age population in all plots for all three Ranunculus species at approximately six-month intervals were tested. The results may be summarized as follows.

Ranunculus repens

Depletion curves for plants originally present in April 1969 in plots A_1, A_2, A_3, B_1, C_1, C_2 and C_3 show significant difference from negative exponential ($p \ll 0.001$ in all cases). Plot B_2 shows no significant difference from exponential (all data from Sarukhan and Harper, 1973).

In all the plots showing significant difference from exponential, apart from B_1, the observed number of plants dying over the first six-month period is greater than expected.

Ranunculus bulbosus

Summary of results of likelihood ratio test:

Plot*	p-value
B_3	+++
E_1	N/S
E_2	+
E_3	++
F_1	++
F_2	N/S
F_3	+++
G_1	++
G_2	++
G_3	+

N.B. : p-values as Table 6.3.a.

* data from Sarukhan and Harper, 1973.

All plots exhibiting a significant difference from negative exponential show a greater than expected loss of individuals over the first six-month period.

Ranunculus acris

Summary of the results of the likelihood ratio test.

Plot*	Number dying over first six-month period		P-value
	Observed	Expected	
D_2 (mature plants)	46	30.1440	+++
D_2 (seedlings)	218	183.7849	+++
D_3 (mature plants)	23	14.8503	++
D_3 (seedlings)	103	79.8000	+++
A_2 (mature plants)	8	4.7805	N/S
G_2 (mature plants)	9	6.6512	+

N.B. : p-values as Table 6.3.a.

* data from Sarukhan and Harper, 1973.

The difference between the observed and expected figures is, on the whole, greater for the mature plants than for seedling cohorts and hence the depletion curves for mature plants are more positively skewed than those for seedlings.

In all three species survivorship and depletion curves appear to have a long "tail". In the case of Ranunculus repens, a note added to the original paper[87] indicates the greater-than-expected longevity of a few plants from the original population.

Thus, in two of the species of this study and in the three species of Ranunculus studied by Sarukhan and Harper, consistent differences from the Deevey type II survivorship curve emerge. These differences appear to support the hypothesis that risk of mortality decreases with increasing age in perennial plants, and are consistent with those reported by Gibbons (in prep.) for Viola rupestris studied in upper Teesdale.

These results receive a fuller explanation in the discussion.

7. SUMMARY

The following two sections summarize chapters four, five and six in terms of their overall effect on the population total and its age-structure over the study period.

7.1 Changes in Population Totals

Figures 7.2.a, I-IV show the changes in the total number of individuals in the population as a cumulative total of numbers in age-classes. Overall population trends can thus be seen by considering the top curve.

Autumn totals have been used throughout, unless stated otherwise, since a longer run of data was then possible. The overall picture obtained is not affected by the choice of season from which to derive a count of total population numbers.

All four populations show a general decline after an initial increase. This is most marked for Draba incana, and least so for the gentian. Both Polygala populations are intermediate between these two extremes in overall changes in total population.

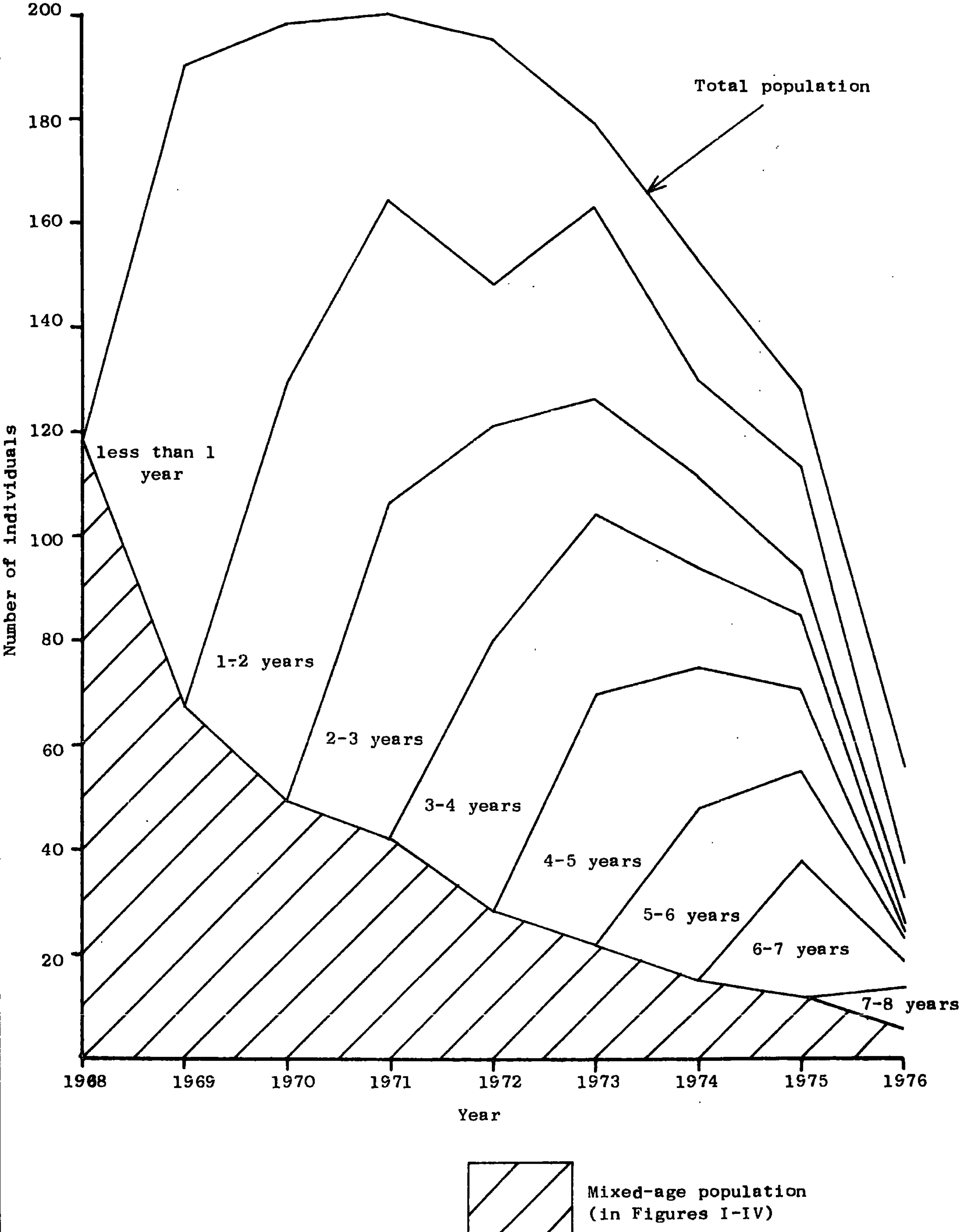
These changes occur as a result of concomitant variation in mortality and recruitment rates over the period of study. Causes are elaborated in the relevant discussion sections.

Highest densities attained are listed in Table 7.1.a. These are also referred to in several discussion sections. Clumping of individuals within plots means that overall densities should be treated with some caution.

7.2 Age-structure

Variation in the age-structure of the populations has been demonstrated. This is represented graphically in figure 7.2.a. Data are not available for Draba incana in 1975.

Nothing is known about the age-structure of those individuals



<u>Figure 7.2.a.I</u> : <u>Polygala amarella</u>, Widdybank : age-structure.

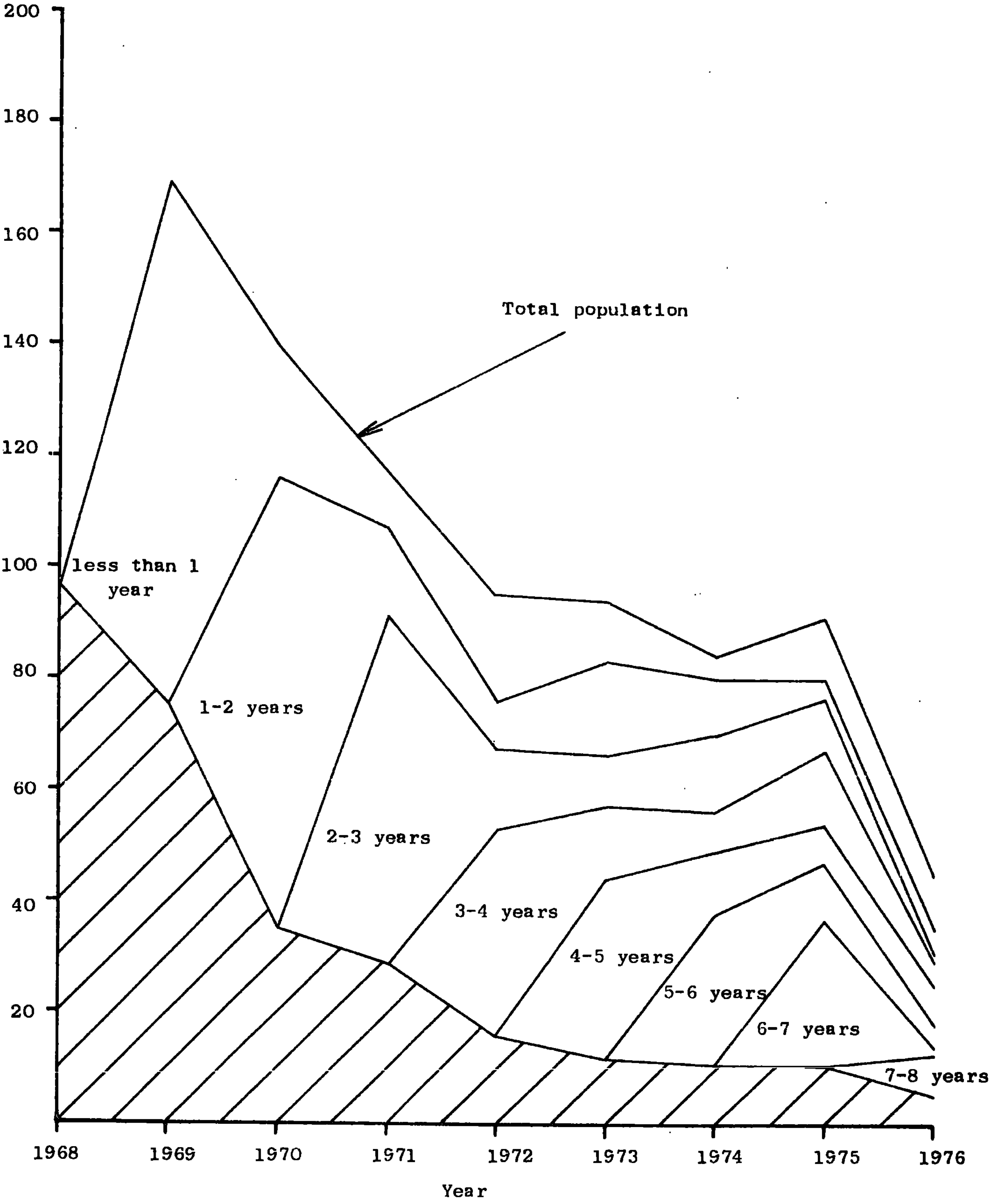


Figure 7.2.a.II : Polygala amarella, Cronkley : age-structure.

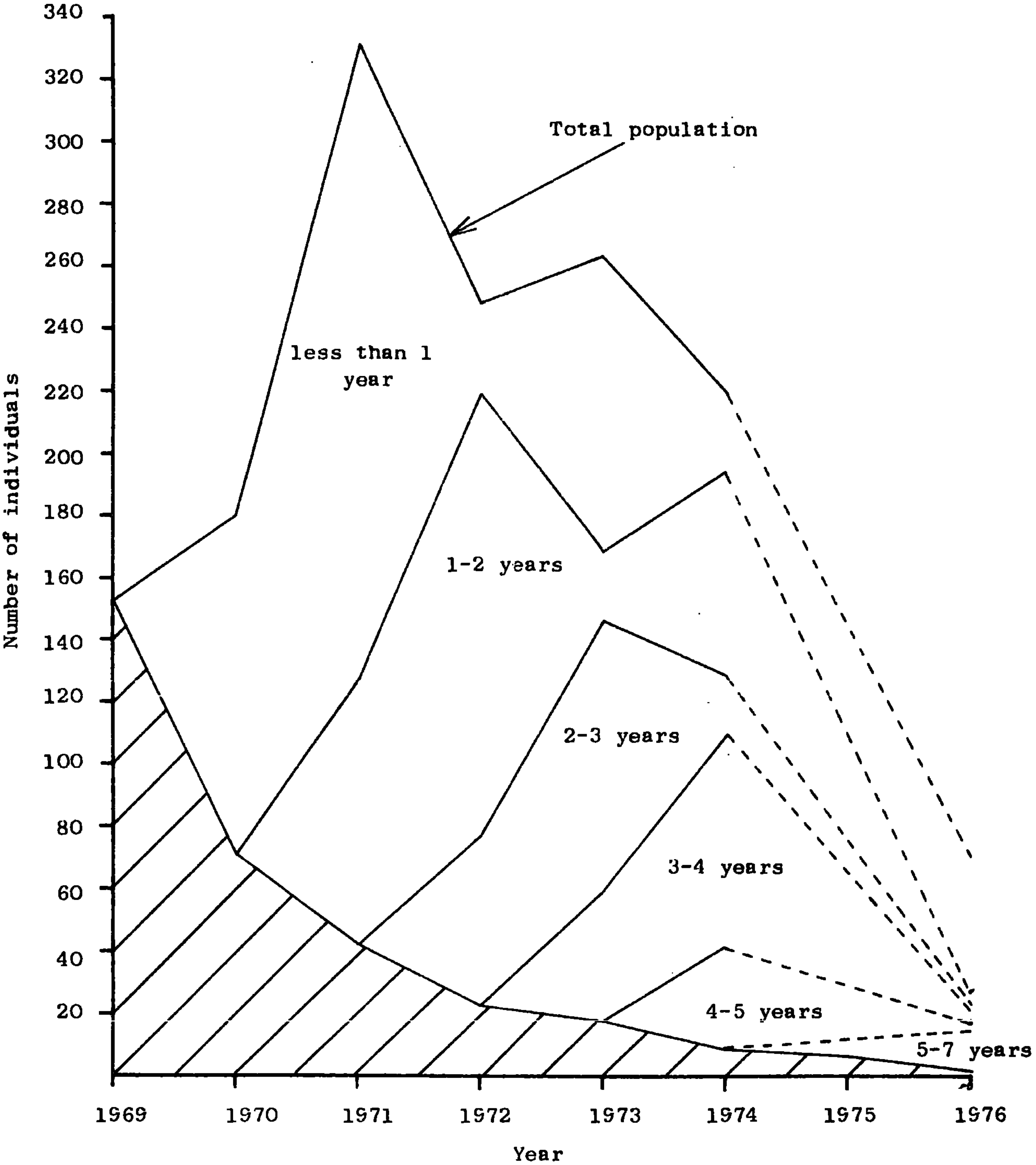
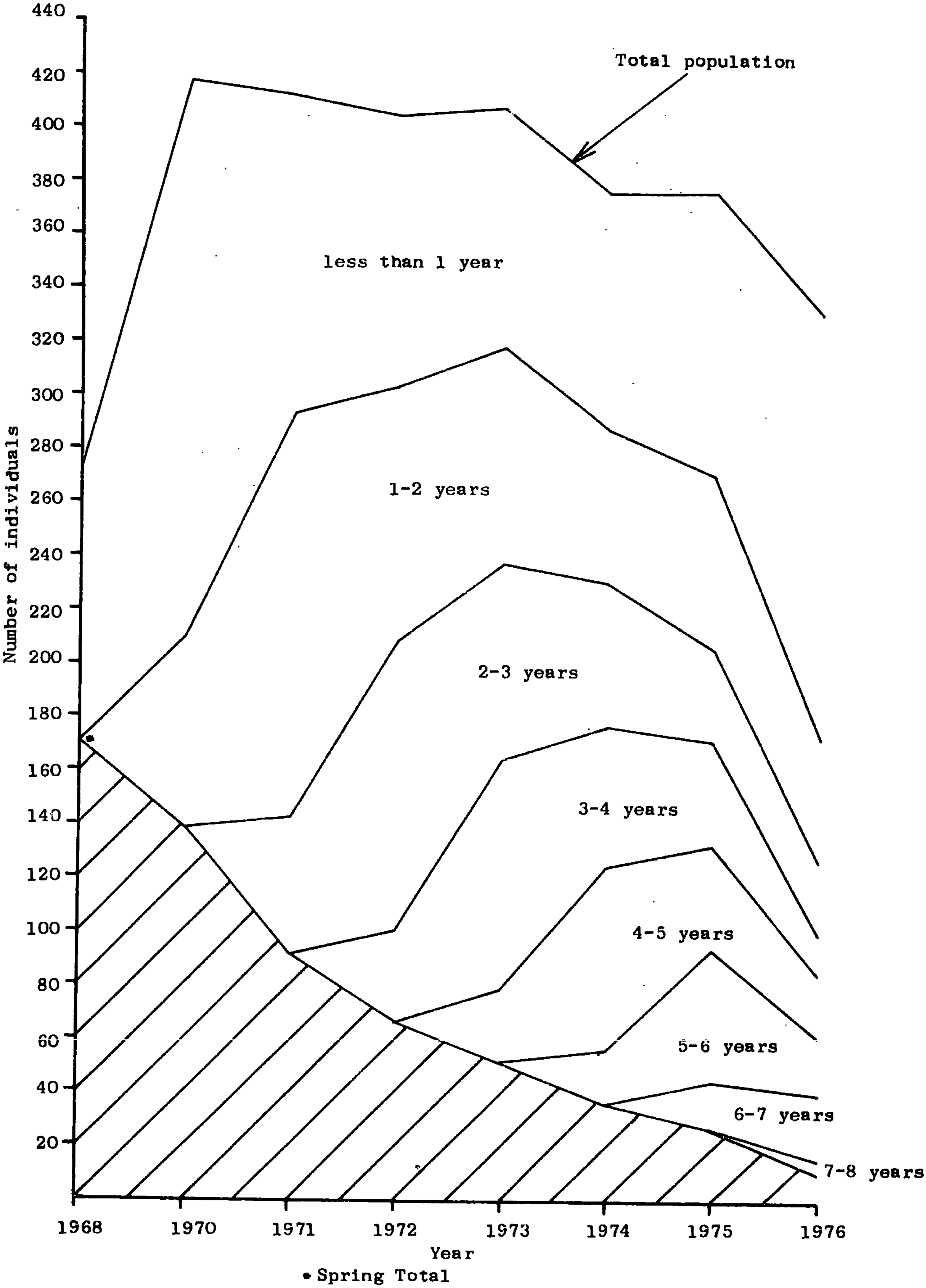


Figure 7.2.a.III : Draba incana : age-structure, (N. B. no record for 1975).



<u>Figure 7.2.a.IV</u> : <u>Gentiana verna</u>, age-structure.

Table 7.1.a : Maximum densities

Species	Maximum Density (no. m^{-2})	Year and Season reached	Total area of plots (m^2)
Polygala amarella (Cronkley)	218.67	Autumn 1969	0.75
Polygala amarella (Widdybank)	77.78	Summer 1971	2.70
Draba incana	124.33	Autumn 1972	1.50
Gentiana verna	136.80	Spring 1971	3.15

originally present in the plots. The lowest curve is the depletion curve of the original, mixed-age population. The hatched area is therefore proportional to the number of individuals of unknown age. As this population is replaced by individuals of known age, progressively more is known about the make-up of the population.

The four populations show some broad, overall similarities. High early recruitment resulted, in each case, in a bulge passing through successive age-classes. This is most clearly seen in:

(a) the 6-7 year age-class of the two Polygala populations, a result of high recruitment in 1969;

(b) the 3-4 year age-class in Draba, resulting from high recruitment in 1971;

(c) the 5-6 year age-class in gentian, a result of high recruitment in 1970.

In all the populations, by the end of the study period, there is a tendency for the younger and older age-classes to predominate.

8. FLOWERING PERFORMANCE

As explained in sections 2.1 and 3.2, the populations described in the previous sections were carefully monitored in the permanent plots, enabling an accurate overall picture of changes in that population over the study-period to be built up.

The plants monitored for reproductive performance are considered to be a separate population. There is no *a priori* reason to believe that the behaviour of these populations mirrors that of the study population. Whilst between-year comparisons of reproductive data are valid, since the sample sites were consistent from year to year, parallels between the populations in the sample sites and those in the permanent plots should be drawn with some caution. Using the only parameters available to compare the two populations, those of total population number, and its pattern of change from year to year, some important differences emerge. These are summarised in Table 8.a. Flowering percentages are calculated from spring totals for gentian, and from summer totals for *Draba* and *Polygala*. Comparison has been made with permanent plot totals at the same time of year, where records are available. Exceptions are noted.

Each section of the table, corresponding to a single year, has one degree of freedom. If differences were purely due to chance, the value of chi-squared for a single year would be expected to equal one. The individual chi-squared values enable the most different years to be picked out.

Overall, the gentian population shows greatest correspondence between the sample site and permanent plot total populations: four years have high chi-squared values, however.

In the other three cases, most years have a great discrepancy, and the overall totals reflect this, giving very low p-values.

Thus, differences have been demonstrated between the behaviour of

Table 8.a : Variation in total population between sample sites and permanent plots

Year:		1969	1970	1971	1972	1973	1974	1975	1976	Total Chi squared	p-value
Gentiana verna	pp	293	330	431	391	369	365	349	293		
	ss	762	812	955	822	849	780	789	787		
	X^2	2.68	0.76	0.68	3.34	0.09	1.75	0.18	4.48	13.29	$0.10 > p > 0.05$
Polygala amarella (Cronkley)	pp	144	138	124	102	92	84	92	45		
	ss	62	246	248	172	167	150	117	109		
	X^2	81.21	1.76	5.45	0.47	1.51	1.10	2.00	6.49	99.98	$p < 0.001$
Polygala amarella (Widdybank)	pp	192	209	210	203	168	153	125	54		
	ss	110	339	570	476	356	376	326	160		
	X^2	131.57	8.44	11.56	2.31	0.08	3.31	4.95	5.33	167.55	$p < 0.001$
Draba incana	pp	152*	161	323	235	258	208	99**	71*		
	ss	191	411	703	569	536	481	96	124		
	X^2	21.29	5.24	0.62	4.24	0.01	1.87	29.16	1.27	63.69	$p < 0.001$

* Spring record
** Autumn record minus seedlings

the two populations in each case. This should be borne in mind when interpreting reproductive data and attempting to relate this to the behaviour of the populations in permanent plots.

8.1 Flowering Percentage

Data for the five populations are presented in Table 8.1.a.

The most striking feature of the figures is the great variability of the flowering of the two Draba and Polygala populations over the period of study. In comparison with these two, gentian has a generally lower, though relatively constant flowering percentage.

Flowering percentage forms the basis of the potential contribution of the established plants of Draba and Polygala to future generations. In gentian, under the conditions in upper Teesdale, seed production makes little, if any, contribution in this way. Most fruits of this species are grazed off, presumably by sheep, on the fell. None has ripened in the permanent quadrats or sample sites, and gone on to liberate seed. Ripe capsules have been found, in small numbers, elsewhere on the fell (Gibbons, pers. comm.).

In the other two species, the ability to flower and set viable seed is crucial in the maintenance of the population, no vegetative means of propagation occurring in either.

8.1.1 Spatial distribution of flowering

Flowering success in Draba has been observed in adjacent strips of the sample site on Cronkley Fell. The whole site measures approximately 8 m by 2 m. The site was divided into three sections in order to count total plants and those flowering. Records were as follows:

Strip	Total plants	Flowering plants	Per cent. flowering
A	115	39	33.9
B	107	15	14.0
C	221	30	13.6
Total	443	84	19.0

Table 8.1.a : Flowering percentages over the period of study

Year	Draba incana				Polygala amarella				Gentiana verna	
	Widdybank		Cronkley		Widdybank		Cronkley			
	% fl	n	% fl	n	% fl	n	% fl	n	% fl	n
1969	32.5	191	-	-	28.2	110	14.5	62	8.8	762
1970	9.9	411	48.8	90	33.3	339	22.7	246	8.3	812
1971	13.2	703	6.7	120	31.3	570	25.3	248	4.7	955
1972	4.6	569	16.8	214	36.8	476	29.1	172	7.8	822
1973	2.4	536	-	-	13.8	356	13.2	167	9.4	849
1974	2.1	481	-	-	10.4	376	10.7	150	8.5	780
1975	5.2	96	-	-	16.6	326	4.3	117	1.8	789
1976	8.8	124	17.1	439	21.9	160	9.2	109	6.4	787
Mean	7.4	389	19.7	216	24.9	339	18.2	159	6.8	820

A and B were each a metre wide and two metres long, occupying the end of the plot with most plants. C formed the rest of the plot. A wide variation in flowering percentage thus exists even between these contiguous strips with a sample site. Once again, the variability in flowering phenomena is emphasised.

No similar observations have been made on Polygala, though it is probably reasonable to assume that spatial as well as temporal variability exists in the flowering of this species also.

8.2 The Survival of Buds, Flowers and Fruits

Both Polygala amarella and Draba incana have been recorded as producing greater numbers of buds, flowers and mature fruits when sown on sugar limestone soil in Durham, as compared with the production achieved on the fell.[21]

Draba seed sown in Durham in January, and plants arising from these, when grown in John Innes compost, have been recorded as flowering within seven months, overwintering and flowering again in the following summer. All plants then died.[10,21] Draba plants in Durham have been recorded as producing up to 72 ripe, mature capsules (mean = 40.3, n = 15). Survivorship between the flower and fruit stage being very high (97.5%) in the same sample (Doody, unpubl. and published results).[21]

The same generalizations can be made about the behaviour of Polygala under more favourable conditions than those found on the fell, though detailed results are not available.

Thus, the maximum inflorescence productivity of both of these species is depressed under general conditions on the fell: an effect of the short growing season. Generally fewer buds are produced and proportionately less of these develop into flowers and fruits. Added to this are losses due to grazing by sheep (on Widdybank Fell) and by sheep and rabbits (on Cronkley).

[illegible]

Table 8.2.a summarizes the inflorescence productivity, after losses, for plants on both fells. Each bud can produce a maximum of one fruit in each case.

With such a variable data set it has not been considered worthwhile calculating mean figures with fiducial limits. The figures do give an indication of loss in reproductive potential between the bud and fruit stage.

The Cronkley population of Draba incana is situated within an exclosure. This is completely sheep-proof, though it is sometimes undermined by rabbits. The higher fruit production by Draba here is undoubtedly a result of exclusion of grazing. This, however, is unlikely to be the only reason. The open, bare sugar-limestone soil on which Draba grows on Cronkley fell appears particularly suited to the plant. Rosettes are generally larger there, and the plants have a more vigorous appearance. This is probably due to the virtual absence of competition, the vegetation is very open, with much bare soil, small plants of Minuartia verna being the only other plant to grow in the area, if at all. On Widdybank Fell Draba is limited to open sites within the grassland: these are often very small and restricted. Plants here appear generally smaller.

The two Polygala populations grow in generally similar habitats on both fells. The site on Cronkley is adjacent to a rabbit warren and plants here seem to suffer the more meticulous grazing of these animals as compared to the plants on Widdybank which have only sheep to contend with. Losses between the flower and fruit stage on Widdybank may reflect loss due to early frosts. It is probable that plants on Cronkley suffer proportionately less losses between the flower and fruit stage because more buds are lost initially (presumably due to grazing) and hence more of the available resources of the plant will be channelled into those flowers which remain.

During 1976, the Polygala sample site on Cronkley was protected

Table 8.2.a.I : *Draba incana*. Production of buds, flowers and fruits per flowering plant

Year	CRONKLEY									WIDDYBANK								
	Buds			Flowers			Fruits			Buds			Flowers			Fruits		
	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n
1969	-	-	-	-	-	-	-	-	-	-	-	-	16.3	3.5	25	11.4	2.0	22
1970	-	-	-	-	-	-	12.8	1.0	34	13.8	1.6	8*	8.8	0.8	12	8.0	0.6	36
1971	-	-	-	12.9	1.2	25	11.8	1.2	25	11.8	0.9	77	9.4	0.7	88	9.1	0.7	88
1972	21.2	3.9	6	15.9	1.1	23	15.4	1.0	23	10.4	1.4	7*	8.8	0.5	60	8.8	0.5	60
1973	-	-	-	-	-	-	-	-	-	11.3	1.5	8*	5.3	1.3	12*	3.1	1.1	12*
1974	-	-	-	-	-	-	-	-	-	16.1	1.7	21	11.8	1.6	24	5.9	1.4	22
1975	-	-	-	--	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1976	20.4	2.5	30	18.7	2.3	30	13.5	1.7	30	13.1	1.0	46	9.0	0.7	46	3.3	0.6	46
Overall	21			16			13			13			10			7		

* sample from one site only

Table 8.2.a.II : *Polygala amarella*. Production of buds, flowers and fruits per flowering plant

Year	CRONKLEY (Pink)									WIDDYBANK (Blue)								
	Buds			Flowers			Fruits			Buds			Flowers			Fruits		
	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n
1969	-	-	-	5.4	1.1	5	3.4	0.8	7	-	-	-	7.8	1.0	25	4.1	0.6	23
1970	11.9	1.2	19	9.9	1.1	19	9.3	1.2	19	16.7	5.0	29	13.2	4.5	29	11.5	4.0	29
1971	9.6	1.1	27	8.5	1.1	27	8.3	1.1	27	14.6	1.4	52	12.4	1.3	52	8.8	1.0	52
1972	7.7	0.6	31	6.9	0.6	31	5.6	0.5	31	13.6	1.2	42	12.1	0.8	42	7.5	0.9	42
1973	-	-	-	-	-	-	-	-	-	17.4	0.9	30	-	-	-	9.0	0.8	30
1974	12.3	1.1	20	9.1	1.0	19	7.3	0.9	18	12.0	0.5	40	6.9	0.4	40	-	-	-
1975	-	-	-	-	-	-	-	-	-	12.1	1.8	24	7.3	1.1	24	5.0	1.1	24
1976	8.6	1.5	11	3.7	1.2	11	3.1	1.2	11	13.3	1.6	24	7.9	0.7	24	4.0	0.8	24
Overall	10			7			6			14			10			7		

from grazing by a wire cage, over 50% flowering was recorded in 1977 as well as good fruit production. Mean numbers of buds, flowers and fruits were 27, 24 and 18 respectively (per flowering plant). This probably indicates that a certain amount of the damage done by grazing is not apparent until the following year: flower initials may be destroyed (if those are formed in the previous year as is common in alpine plants); or flowering be depressed due to removal of all or part of the photosynthetic organs. Either of these two effects acting over the study period would have resulted in the differences observed, after protection, in 1977. Large numbers of capsules matured, the ground surface appearing literally strewn with capsules.

High flowering percentage has continued in 1978, and good recruitment has been observed from seed set in 1977 (Bradshaw, pers. comm.).

8.3 Proliferation of Inflorescences

As was mentioned in section 3.1, individuals of Polygala and Draba may produce several inflorescences. The same is not true of gentian which, if it flowers, only produces a single capsule per rosette, at the most. Each inflorescence of the other two species is itself indeterminate, growing on until growth is halted by frost.

The proliferation seen in Polygala and Draba seems to occur as a result of damage to the terminal bud, usually by grazing animals. Both plants may then produce several inflorescences.

In Draba these grow from the axillary buds of the rosette leaves, occasionally resulting in large numbers of capsules being borne by one plant. Late in June, 1977, one heroic individual was found to be bearing 116 fruits on nine separate inflorescences!

Plants of Polygala amarella have been seen with up to six separate inflorescences (Bradshaw, pers. comm.).

It should be stressed that in both species this is not a common occurrence. Of the eighty-odd individuals of Draba observed in 1977 only the one noted above produced more than one inflorescence. It was never observed in Polygala during that year.

8.4 Age at Flowering

In each case, the oldest cohorts only have been used to determine age at first flowering in order to avoid bias towards a younger flowering age, which would result from using all plants of known age.

The results are expressed in figure 8.4.a.

Exceptionally, individuals of Draba incana may produce inflorescences in successive years. This has occurred when the first inflorescence has been grazed off before it had matured. Hence, in terms of its contribution to future generations, the individual is always monocarpic.

Both gentian and Polygala, however, may produce inflorescences in successive years. The following data on flowering in these two species are summarized from Gibbons (in prep.).

Polygala amarella

About 80% of rosettes on Cronkley and 90% on Widdybank do not flower at all. Of those that flower 22% die having flowered once on Widdybank, whilst 43% die on Cronkley. This probably results from the grazing pressure, as noted in section 8.2. Only seven plants have been recorded as flowering twice on Cronkley whilst twenty-one did so on Widdybank. In the latter case twelve plants went on to flower three times and one plant flowered four and five times.

Gentiana verna

About 70% of rosettes died without flowering; 20% lived through the study period without flowering and only 10% of rosettes flowered.

Of those flowering, 45% die within a year of doing so, and 13% go on to flower twice. No plants were recorded as flowering three times.

Draba incana

No plants have been observed to flower having had an inflorescence

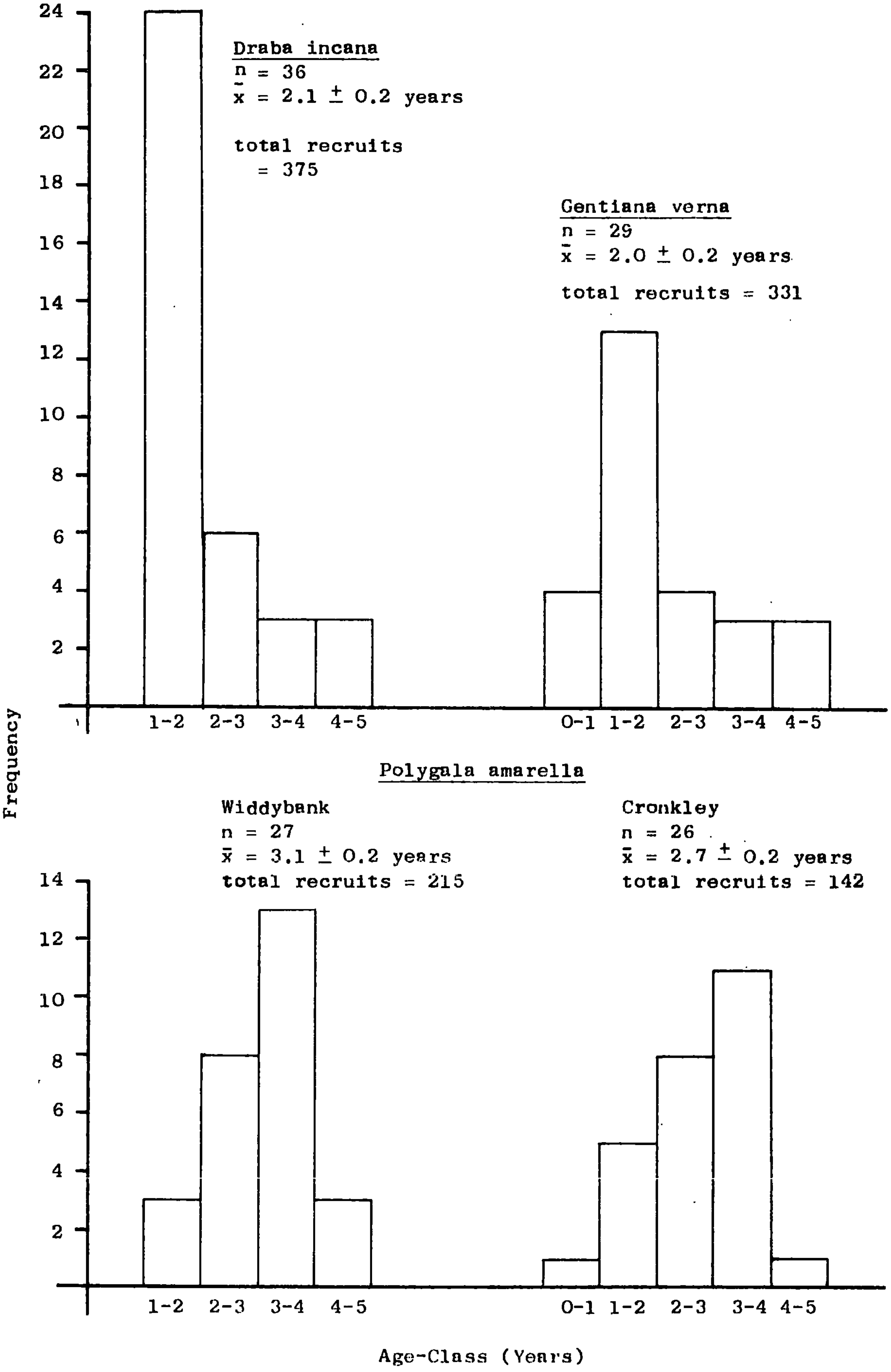


Figure 8.4.a : Age at first flowering of plants recruited in 1969 and 1970.

mature in the previous year.

About 90% of the 1969 and 1970 recruits died without flowering.

8.5 Dispersal of Seeds

No critical observations have been made on any of the three species. The following account is based on "circumstantial" evidence from observations on germinating seed, some experimental work already described and a consideration of the seed size and weight of the three species concerned, in addition to relevant literature.

Doody[21] considered that dispersal of seeds of Draba incana was "... limited to a small area around the parent plant". This now appears unlikely. Removal of seed from the experimental germination sites, probably by wind, implies that seeds do not remain where they originally fall from the parent plant, but can be transported some distance afterwards. Dispersal appears to take place over a protracted period in this species. Long after the valves have fallen from the capsule, seed remains attached to the replum, in situ on the dead parent plant. Seeds seem to be lost in ones or twos from this position. They may be elevated up to about ten centimetres from the soil surface during this period, probably high enough for the strong winds characteristic of the fell-tops to achieve quite wide dispersal. The rather prosaic description of Ridley[83] is probably more appropriate. He considers that "... the oval, thin replum on its springy pedicel blown by the wind sends the seeds away like tennis balls from a racket" (sic) (describing Draba verna).

Ridley notes that seeds of Gentiana nivalis and Gentianella amarella pass through the gut of sheep and out, with the excreta, undamaged. It is, therefore a possibility that seeds of Gentiana verna are dispersed in this way, and apparent losses due to grazing are not the only reason for the low numbers of seedlings establishing on the fell. The seeds themselves are smaller than those of Draba and are probably even more widely dispersed than the latter by the action of wind alone.

Polygala amarella, which has much larger seed is unlikely to have them distributed by the wind in the way that the previous two species are. Ripe capsules fall from the inflorescence with the seeds still inside. They are commonly found near the parent plant, and Doody[21] records seedlings growing very close to a plant which had flowered in the previous year. On Cronkley and Widdybank fells, the inflorescences of Polygala do not commonly extend to the length seen in the Craven plants. Protection from grazing in 1976 did, however, result in greater elongation of the inflorescence. This altered the character of the fruiting plant considerably and it became obvious that the pendulous stem could distribute capsules several inches away from the parent plant. In addition, the seeds themselves have an elaiosome, or oil body. Ridley[83] notes the importance of this structure in seeds of Polygala vulgaris: "This oily substance is very attractive to ants, and they seek for seeds and fruits so furnished, and carry them to the nest, very frequently eating off the oil body on the way and then dropping the seed". It is possible that the same occurrence takes place in the study areas.

9. INTRODUCTION TO DISCUSSION

The results will be discussed with reference to two central problems in plant demography: the definition of the individual, and the adaption of life-strategy to the environment. This section outlines the issues involved before taking them up in discussion.

9.1 The Individual

In placing the emphasis on the functional unit as the individual in the population, attention has been focussed at that level of organization which is alone capable of replication, be it by sexual or vegetative means. The rooted rosette, in each of the three species, is that unit about which the dynamics of the population is centred.

If population dynamicists place the emphasis on the genetic individual[36,38] then, in the case of vegetatively reproducing species, this will require further qualification. Harper and White (op. cit.) suggested N_{η} as a symbolism sensitive to this requirement. N represents the number of genets and η the number of ramets, or other subdivisions of the genetic individual: leaves, fruits, etc. However, when the central concern is one of numbers, the individual should be defined in terms of the contribution which it can make to future numbers in the population. The individual is most instructively seen as that unit within the population having the potential to reproduce its form either by sexual or vegetative means, or both, depending on the species under consideration. If the individual ramet has the potential to contribute to r, the intrinsic rate of natural increase of a population, independently of its parent, it must be regarded as an individual in its own right. It does not increase the longevity, and therefore the reproductive potential, of its parent in a sense meaningful to plant demography, since it is individually capable of an independent contribution to r.

The issue is partly one of time-scale. The demographer is concerned with changes occurring over relatively few generations. Interactions between the genotype and the environment, of great concern to the population geneticist, are a fairly constant factor over the time-scale of most plant demography studies. The emphasis on the genetic individual seems misplaced. Situations with high selection pressures, such as those described by Antonovics[1] and Antonovics and Bradshaw,[2] are exceptions to the general situation in which most plant populations survive.

These observations are made from the standpoint of the species under consideration which, as has been noted (in 3.1) have a fairly canalized rosette-form. Exceptions to this form provide some means of examining the use of this definition of an individual. They are discussed most fully in connection with the longevity of older plants and production of inflorescences.

9.2 Adaptive Strategies

This branch of ecology, which seeks to encompass all stages of the life-history of a plant and relate them to the particular constraints of its environment, has gathered momentum very quickly in the last few years. For plant demographers it offers the possibility of placing observational and empirical evidence within an all-embracing theory of the dynamics of populations.

Its fundamental starting point is the logistic equation for population growth:

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

where: N is the number in the population,
t is time,
r is the intrinsic rate of increase,
K is the carrying capacity of the environment.

Thus the rate of growth of the population is dependent upon the (environmentally mediated) degree of realization of the instrinsic rate of increase. The degree to which either r or K predominates in the overall adaptive strategy of a population provides a useful shorthand with which to describe its demography.

Harper[36] points out that even under carefully controlled experimental conditions, using unicellular organisms, departures from the logistic curve are commoner than conformity. The model is, nonetheless, important to the conceptual basis of population dynamics. As Harper (op. cit.) says:

> "The logistic curve remains central to population biology not because it describes how populations behave but because it provides a standard base of ideal behaviour against which the reality can be judged and measured." (p. 3)

The original theory of r- and K-selection was pioneered by MacArthur and Wilson in "The Theory of Island Biogeography".[60] It was expanded by Pianka[75] and given a theoretical mathematical basis by Gadgil and Bossert.[25] The theory envisages an ecological continuum which has, as the r-endpoint "a perfect ecologic (sic.) vacuum with no density effects and no competition"[75] and as the K-endpoint an environment containing populations at maximum density, exploiting resources to the full.

Organisms adapted to these theoretical extremes have distinct strategies which fit them to their environment. r-adapted species, broadly, have rapid development to maturity; early reproduction; small size and high productivity (seed output). K-adapted species, on the other hand, take longer to reach maturity; have low reproductive effort, often spread over successive seasons, and consequently a lower value of r.

The critical difference between the two strategies is in the proportion of the total energy resources of the plant which are allocated to reproduction.[66] High reproductive potential implies greater reliance on the establishment of new individuals for the survival of the population, whilst high energy allocation to non-reproductive tissue implies reliance on the persistence of the individual to maintain the population. The concept is not referable to absolute differences, but is of most value in comparing the position of two species, or biotypes, along a hypothetical continuum between r- and K-adaptation.[26] Gadgil and Solbrig (op. cit.) regard the magnitdue of density independent mortality as the crucial factor in r- and K-selection. Reliance on resource partitioning and a direct causal link between density independent mortality and overall strategy has led to the criticism of the concept[34,67,68] on the grounds of incompleteness, as has the lack of experimental evidence. Moore[68] states that most evidence is circumstantial. Recent experimental work on dandelions[91,92] has gone some way to remedy this, providing results which support the theory.

More recently, Grime[32] has refined the concept, suggesting three fundamental selection pressures.

1. C-selection which favours highly competitive ability dependent on maximal vegetative growth in relatively undisturbed habitats (competitive);
2. S-selection which reduces both vegetative and reproductive vigour and favours adaptations which will allow survival over stressed periods (stress-tolerant);
3. R-selection which favours a short life-span and high seed production (ruderal).

The three strategies: competitive, stress-tolerant and ruderal have evolved in response to three selection pressures which are seen to be linked as shown in figure 9.2.a. The primary selection pressures are carefully defined, viz.:

competition : "The tendency of neighbouring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water or volume of space."[30]

stress : "External constraints which limit the rate of dry matter production of all or part of the vegetation."[32]

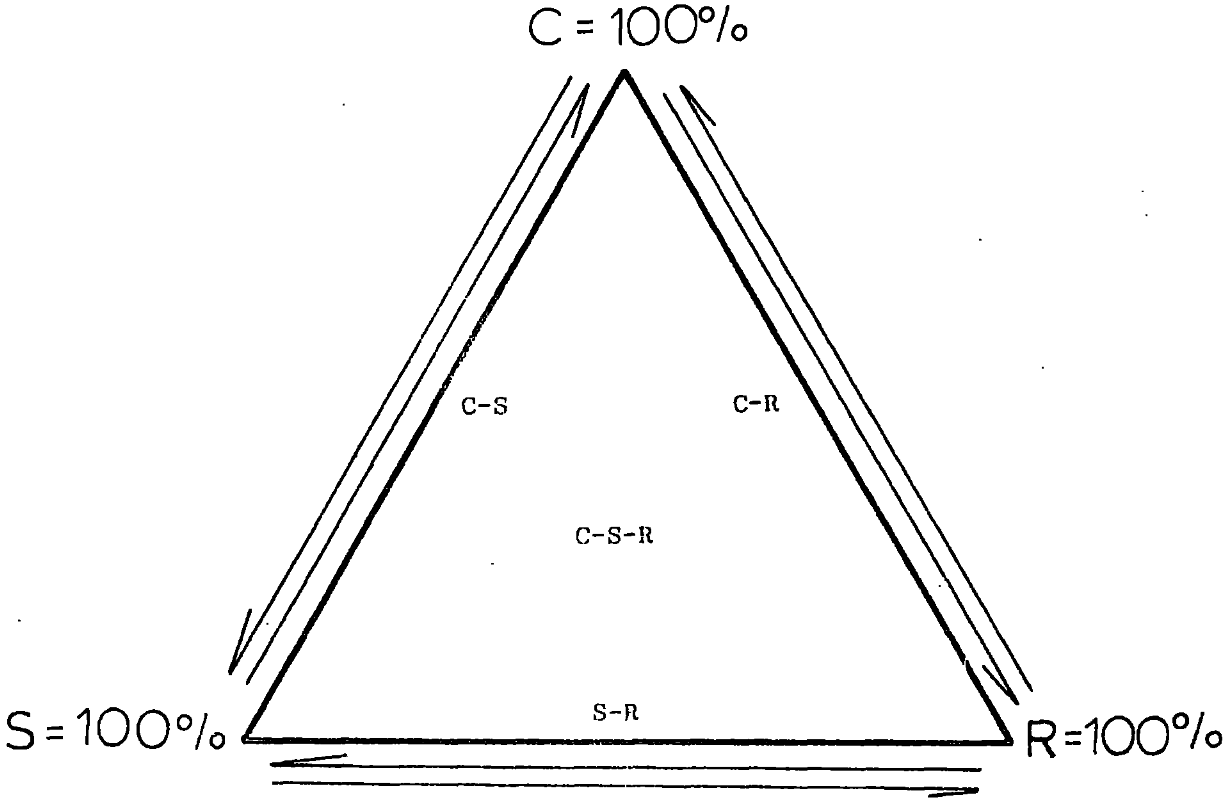


Figure 9.2.a : The relationship between the three primary strategies, showing the four secondary strategies (adapted from Grime, 1974 and 1978).

disturbance : "Mechanisms which limit the plant biomass by causing its destruction."[32]

This theory is a refinement of the original r-, K-theory to which it is linked as shown in figure 9.2.b.

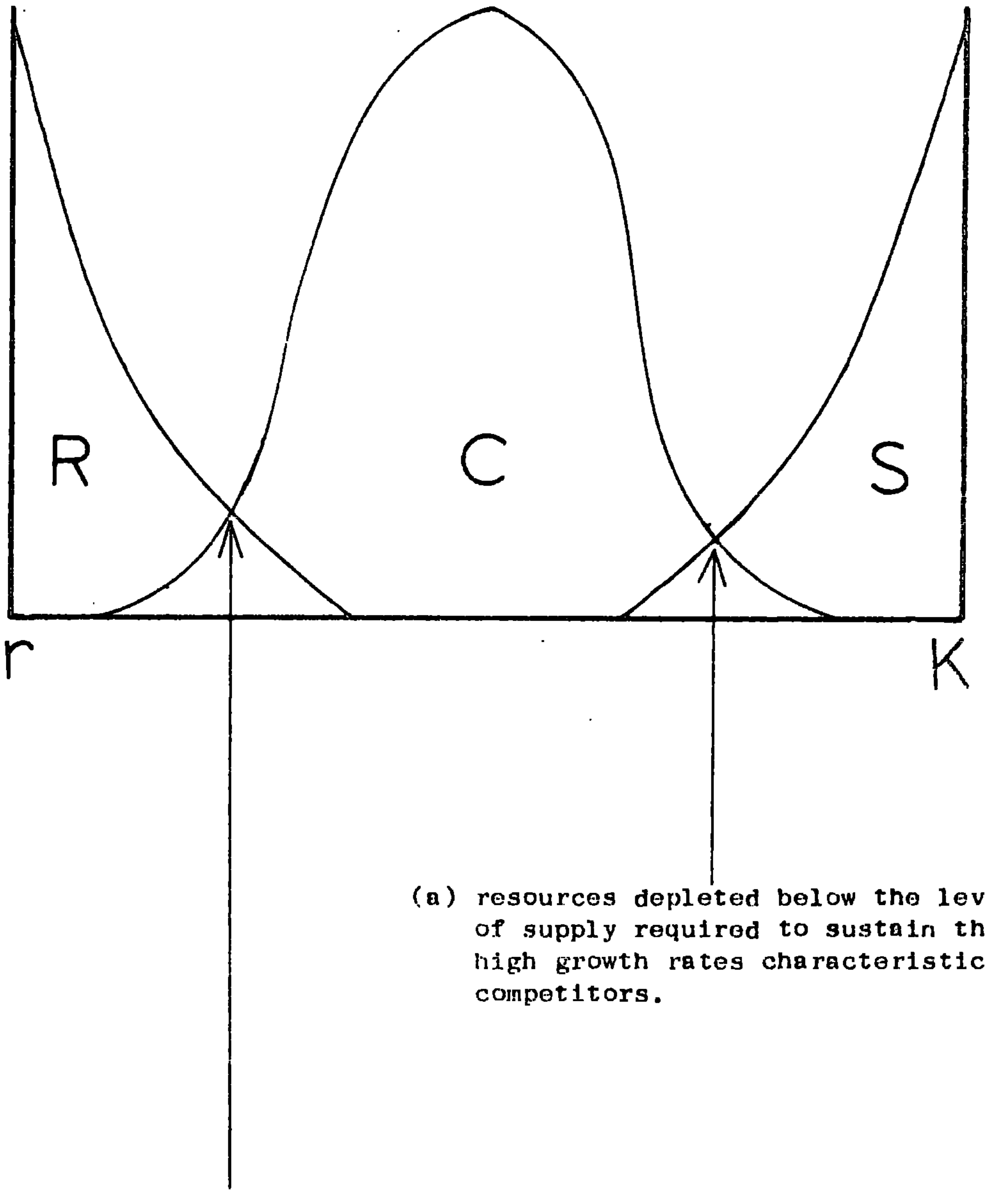
Grime identifies two important points in the model: where the selective advantage shifts between two strategies (see figure 9.2.b).

Besides providing a more sensitive and complete model, experimental evidence is accumulating by which it can be tested and used. Grime[31] has used this model with an index of competitive ability (incorporating height of canopy, lateral spread and litter accumulation) and an index of R (maximum relative growth rate measured in the first two to five weeks after germination, R_{max}) to construct an ordination of plant communities based on the strategies of component species.

Careful measurements of plant growth parameters are shifting the emphasis away from the partitioning of photosynthate between simply vegetative and reproductive organs, and attempting to relate the value of R_{max} to differences in plant structure.[33] High R_{max} in competitors leads to rapid assumption of tall stature, lateral spread and litter accumulation necessary for efficient capture of light, water and mineral nutrients. In ruderals it leads to rapid completion of life-cycle, with a larger proportion of the photosynthate being channelled into seed production.

Low R_{max} is considered to be an adaptation to stress, modest demands and resulting low growth rate being suited to extreme and protracted stress. A low rate of energy accumulation in structure may allow a greater build-up of reserves, to be metabolized over a period of harsh conditions.

Grime and Hunt (op. cit.) conclude that the significance of high R_{max} extends beyond simply dry matter accumulation, its importance includes "... great plasticity in the deployment of photosynthate between root and shoot and a rapid response to environmental variation especially in the



(a) resources depleted below the level of supply required to sustain the high growth rates characteristic of competitors.

(b) disturbance prevents exclusion of ruderals by competitors.

Figure 9.2.b : The relationship between the two theories of plant strategy (after Grime, 1978).

extension growth of stems, petioles and roots and in the expansion of leaf area".

It is proposed to compare the strategies of the three species of this study in the light of this theory. Unfortunately, the observational data will still merit the criticism of Moore: that of being circumstantial. Gibbons (in prep.) by using between-site comparisons within a population is able to shed some light on intra-specific variations in strategy. Such an approach is beyond the scope of the present work.

Grime's broad definitions of the primary selection pressures enable the fell-top environment to be put in an overall framework. In discussing arctic-alpine environments he says;[32] "the most conspicuous effect of severe stress is to eliminate or debilitate species of high competitive ability and to cause them to be replaced by stress-tolerant species". This is undoubtedly the case in upper Teesdale (see section 1.4), and provides an overall framework within which to consider the species. Thus, the C-S-R theory overcomes one of the criticisms of the r-K theory, that of its limitation to comparative questions, and will stimulate a more rigourous, quantitative approach to plant strategies and resource partitioning.

Harper[36] notes the relative paucity of information on herbaceous perennials, and since these plants exhibit the greatest range of adaptive strategies,[32] many gaps exist in our knowledge. Hopefully, the present study will go some way to overcoming this and, concentrating as it does on plants in a sub-arctic environment, provide some balance to the accounts most prevalent in the literature which concentrate on woodland or temperate grassland species.

10. GENETS, RAMETS AND RECRUITMENT

Reproduction in seed-producing plants is potentially a very wasteful process. Thompson[98] records high losses of buried and non-buried seeds from a wide variety of species in woodland, grassland, marsh, hedgerow and man-made sites. He also emphasises the loss inherent in wind-dispersal mechanisms, which is recorded by Salisbury.[86]

The first stage in what is a fairly conservative strategy of seed production in Polygala and Draba is the predominance of selfing. Genetic variability is sacrificed, presumably with an increased probability of saturation of ovules with pollen. A fertilization rate of 96%* was recorded for Draba in 1976 on Widdybank Fell, 74% being recorded in 1977. In the latter year 81% of ovules of this species were fertilized on Cronkley. Ovule number (per capsule) has been demonstrated to be constant in this species, and higher on Cronkley than on Widdybank.

In this context it is interesting to note that the site on Cronkley is much more disturbed than those areas where Draba is found on Widdybank Fell. The potential to produce larger numbers of seeds has been noted in biotypes adapted to more disturbed conditions.[92] Seeds from plants growing in these conditions are lighter, to facilitate greater dispersal and thereby increase the probability of encountering suitable sites for germination. Though Draba on Cronkley grows in the more disturbed situation, its seeds are heavier here than those from plants on Widdybank Fell. This is probably a function of the low competition experienced by the plants on Cronkley, very few other species being able to colonize the immature sugar limestone soil. Seed size and weight in this species seem to be far

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* Figures not included in results. Site 2 had maximum fertilization rate: 97.2%.

more plastic than seed number per capsule and is presumably a function of the environment and the vigour of the parent plant. The low viability of seeds on Cronkley in 1977 may have been a result of the very hot summer of 1976. Many plants had large numbers of scorched basal leaves throughout the whole of the 1977 growing season and it is a possibility that seeds did not mature because of abnormally low photosynthate production. If so, this emphasises the marginal threshold at which photosynthesis operates in this stressed environment. Plants on Widdybank were not scorched in the same way and had good production of viable seed in 1977. The occurrence of a pathogen outbreak on Cronkley in 1977 cannot, however, be discounted.

From the data available the development of seed within the capsule seems to have a high success rate, when considered over the whole period, viz.:

Species and Site	Viable seed* as percentage of ovules
Gentiana verna (Widdybank)	70
Draba incana (Widdybank)	87
Draba incana (Cronkley)	85
Polygala amarella (Widdybank)	75
Polygala amarella (Cronkley)	80

* data from section 4.1

It seems likely that the large numbers of non-viable seed produced by *Draba* on Cronkley is an uncommon occurrence. Examination of seed collected over a number of years dating back to 1968 did not reveal seed which (to a visual examination) appeared non-viable.

Polygala seed seems to have a high percentage viability[21] though the very limited numbers of plants on the fell have prevented removal of seed for exhaustive tests.

Harper[36] considers that most plants over-produce the number of seeds which they initiate, reducing this number by abortion at an early stage in the development of the seeds in response to environmental stress. Thus if photosynthate is limited, some internal mechanism controls the number of seeds which grows and the size is maintained fairly constant. A large percentage viability is expected in stress-tolerant plants since these would not theoretically be expected to commit resources to a wasteful mechanism of seed production.

Draba has been regarded as an "opportunist" species,[9,10,21] but while this is true in the contex of the Teesdale rarities, it is not so in comparison with other grassland species for which five thousand seeds per plant would be a common figure.[85] Seen in this context the overall seed production of Draba, 245 seeds per plant on Cronkley and 122 seeds per plant on Widdybank, is quite modest, precisely what would be expected in a stress-tolerant species.

If an estimate of the weight of a full crop of seeds from a single plant per year (the product of: maximum capsule number per plant; mean seed number per capsule and mean seed weight) is calculated for Draba and Polygala, the output is 33 mg and 28 mg respectively. The way that these similar amounts of resources are distributed between seeds is, of course, very different. Draba is a plant of very open habitats and, as such, need not invest large amounts of energy in each seed: those which fall in dense vegetation are doomed to failure and those which fall on open soil will not suffer from the competition at the seedling stage which necessitates a large food reserve. Polygala, on the other hand, is a plant of the closed grass sward, often growing under dwarf shrubs: Calluna vulgaris and/or

Empetrum nigrum. Hence if each seedling is to survive, it must have a large food supply and be able to produce large cotyledons upon germinating to enable it to begin to photosynthesise in a somewhat shaded niche.

From the observations made on germination it would appear that neither *Draba* nor *Polygala* has innate or induced dormancy but that germination is prevented by, presumably, low temperatures. Billings and Mooney,[7] commenting on the harsh over-winter conditions encountered by arctic-alpine plants say, "one might anticipate finding almost universal seed dormancy as a positive mechanism, but such is not the case. Given a suitable environment in the laboratory, fresh seeds of most alpine and tundra plants germinate rather easily". They go on to say that most seeds germinate in the year following seed set. It would appear that the same is true in *Polygala* and *Draba*. The gentian behaves quite differently having a chilling requirement and a low rate of germination spread over several years after seed-set.[22]

Seeds of both *Draba* and *Polygala* have been observed to germinate on the fell in autumn. Before chilling, seeds of *Draba* rapidly germinate to almost 100%, but after cold treatment the rise to the maximum germination rate is slower. This mechanism would favour rapid germination and establishment in the autumn, probably to achieve maximum seedling growth before the cold months. In the spring, seeds having survived over winter on the fell would germinate in a far more cautious manner and in this way maintain the maximum chance of some of the seedlings avoiding the late-spring frosts which are common on the fell.

Thompson,[98] considering the high mortality characteristic of many buried seed populations, argues that there would be strong selection pressures against such a strategy in stress-tolerant species, where seed output is limited. He considers "the development of a bank of seedlings represents a mechanism of ensuing regeneration under conditions in which seed production is too small and infrequent and the environment is insufficiently productive and disturbed to sustain the other types of regeneration strategies" (i.e. from buried and non-buried viable seed).

Experimental evidence and limited observations on the fell suggest that this strategy is a possibility. The relatively large numbers of spring recruits of Polygala could conceivably have survived in such a manner over winter. Further observations are necessary to clarify the situation in the study species. Grime[32] has suggested a priori that stress-tolerators would be unpalateable, low R_{max} values not enabling tissue to be replaced, if damaged. This would be an advantage to a standing bank of seedlings.

Some attempts have been made to isolate and germinate seeds of Draba incana from soil collected on Widdybank Fell (Marren, unpubl.). These were unsuccessful. Thus, the evidence suggests that neither Draba incana nor Polygala amarella has a buried seed store. This makes the occasional high recruitment of Polygala, which has already been noted as significant in the maintenance of its populations,[9,10,21] of even greater importance if its survival on the fell is to be ensured.

It is difficult to relate the Draba germination experiments on seed of different ages to the situation on the fell. Attempts to germinate seed over seven years old were unsuccessful. A gradual decline in viability with age seems likely when seed are stored under lab conditions. A much greater rate of loss of viability would be anticipated on the fell.

The inability to obtain a correlation between seed size and percentage viability in fresh Draba seed may suggest that this effect is only manifest in older seeds, and, therefore, that larger seeds have a better survival rate. Once again, it is difficult to see these results as being relevant to the situation on the fell.

Germination and Establishment

Having considered the seed population in connection with germination, it is now proposed to attempt to relate some of the experimental work to the environment of the seed, the existence of Harper's so-called "safe-sites".[36]

As Harper (*op. cit.*) emphasises, the scale of heterogeneity which one must consider is that determined by the size of the seed: "a worm-cast is a mountain to a mustard seed ... a rain-drop is a cataclysm".

The difficulty with which this heterogeneity is appreciated is ably demonstrated by the complete failure of the fell-top germination experiments on *Draba incana*! (See section 4.2.3.) While care was taken to select sites which appeared to be suitable for germination, no seedlings were recorded. This emphasises the great element of chance which restricts the number of *Draba* seedlings germinating on the fell. An observation outside the experimental plots corroborates this: approximately fifty seedlings were seen close to site 2 on 31/V/1977. These had germinated in a dense cluster similar to those recorded by Doody.[21] All these seedlings had successfully produced the buds of the first true leaves, and most of those which were less densely packed had produced four true leaves. When seen a few days later all these seedlings appeared desiccated, and none remained by 23/VI/1977. Evidently a site which was suitable for germination did not prove suitable for establishment, possibly due to a brief spell of dry weather leading to drying of the soil and desiccation of the seedlings before deep root growth had occurred.

Some of the laboratory experiments on *Draba* seeds are useful in considering the effect of the substrate on germination.

Overall percentage germination is lower in John Innes compost than on sugar limestone soil and the time taken to reach maximum germination percentage is much quicker in the latter, though onset is delayed.

Significantly less seed germinated when mixed with baked sand than that sown on to filter-paper in the lab.

Light is known to be a factor necessary to the germination of Draba seeds. When a clean filter paper, light at all wavelengths would be reflected around the seed, in addition to that incident on the seed itself, John Innes compost and sand would have two effects: since seed may become lodged below the surface less incident light would impinge on it; and the dark compost would absorb most of the wavelengths of light (this would occur to a less extent in sand).

Harper and Benton[37] have shown that particle size also affects water availability. This is unlikely to be an effect of the sand in the laboratory experiments since water was supplied to form a visible layer over the surface of the seed/sand mixture. Water tension was probably zero, though could not be measured under the conditions of the experiment.

The importance of the effect of particle size on water tension is likely to be quite important on the fell. Some of the seeds at one of the germination sites were observed on the surface for several weeks and had not imbibed. Harper et al. had earlier shown that microtopography of the soil surface could shift the balance of numbers of seedlings of two species of Bromus germinating from a seed mixture containing equal proportions of each.[39] This was an effect of topography on the orientation of the seed on the soil, which affected subsequent growth and establishment.

Significantly better germination of Draba seed has been demonstrated on south-facing sites on the fell. The John Innes compost in which the trials were sown is much darker than the bare sugar limestone which forms the preferred habitat of this plant on the fell, and thus temperature differences due to heat absorption would be more marked. Nonetheless there is an indication of another factor which is important in ensuring germination on the fell.

On the whole it can be seen how great a part chance plays in the distribution and subsequent successful germination of Draba seedlings on the fell. The same would also be true of Gentiana verna which produces larger numbers of even smaller seeds. Gibbons (in prep.) considers that there is a strong selection pressure against flowering in gentian on the fell-top. Plants at another (lower) site have a greater annual flowering percentage. The channelling of resources away from a wasteful strategy of seed production and into a less risky mode of reproduction follows the theoretical framework being built up around C, S and R-selection.

Seeds have been demonstrated to affect the environment of others nearby. Both positive and negative responses have been shown, and these have been related to the overall strategy of the plants concerned.[59]

Seeds of Draba incana were sown at three densities in John Innes Compost in 1970 (Doody, unpubl.). There is some indication that at the highest density there is promotion of germination ($0.1 > p > 0.05$). In the laboratory experiments at differing densities the seedlings at higher density appeared further advanced than those at lower: the hypocotyl appeared longer and cotyledons larger. Unfortunately, follow-up experiments were impossible due to lack of seed, but this may well be a productive area for further study. It is particularly interesting in Draba since a density-dependent germination strategy might account for the large numbers of seedlings growing together reported by Doody.[21] It can be viewed as a mechanism for promoting the development of a standing bank of seedlings, assuming the latter is advantageous (see before).

Linhart[59] envisages the following advantages:

(a) reduction of fluctuations in temperature and moisture;

(b) breaking up of soil by the concomitant effort of several radicles;

(c) increases the chances that at least one would survive to reproduction.

The more rapid germination and growth of seedlings from larger seed has been noted in Draba incana. It is possible that this provides a mechanism by which one seedling in a cluster will establish more successfully than the rest while still obtaining protection from those around it. Even growth of all seedlings in a cluster is more likely to lead to the death of all. It has been demonstrated that the smallest plants in a population are the first to thin,[109] thus immediate post-germination growth will intensify any disparities between seedlings due to seed size or the suitability of the "safe-site".

Linhart (op. cit.) notes that seeds germinating together are likely to come from the same plant and continues, "... the more rapid occupation of a favourable site by a stand of related individuals ... may provide a competitive edge over other unrelated and slower germinating individuals".

The high early mortality of Draba seedlings has been referred to as a result of "self-thinning"[9,10,21] but whether high initial mortality is a result of competition between seedlings or with the surrounding vegetation is not clear. This term, coined by Yoda et al.,[111] originally referred to pure stands in experimental and crop studies and is misleading when applied to natural vegetation, where alien thinning is likely to occur.

With such high losses between seed set and establishment it is not surprising that Bradshaw and Doody[10] conclude, of Draba incana, that "the species remains ... localised and certainly does not occupy all apparently suitable sites".

From the data presented in the results an estimate of the loss of Draba seeds before seedling establishment (i.e. up to six months after germination) can be made. An imaginary cohort of 1,000 seeds would leave only 47 seedlings of age six months.

Polygala amarella on Widdybank Fell would leave 232 seedlings from 1,000 seeds; and on Cronkley 193.

The larger seed of Polygala are an adaptation to growth in closed vegetation. From the time that a seedling becomes visible in the permanent plots, it has the same mortality rate as older plants. Pre-emergence losses, as might be expected, are higher. The causes of the latter are unknown and may be due to seed infertility, predation or lack of a stimulus to trigger the germination response. The filtering of red wavelengths of light by the vegetation of a closed sward has been noted,[34] and such a mechanism could operate to prevent the germination of *Polygala* seeds.

The good survival of seedlings of this species is an adaptation to the stressed environment.

Low seedling viability is seen by Harper[36] as the dumping of a proportion of genetic experiments: those badly adapted genotypes resulting from recombination. Since selfing in *Polygala* restricts the amount of genetic variability in the seed produced, a large wastage would not be expected; and whilst *Draba* appears to have a wasteful strategy in comparison with *Polygala*, when compared to other grassland species it is clearly fairly conservative. *Draba* is a more R-adapted plant in its seed production and recruitment strategy than *Polygala*, but overall they both behave in a manner best explained as stress-adapted.

Gentiana verna has the lowest overall flowering percentage of the three species, and since only one flower is produced per rosette, probably partitions the smallest amount of its resources into flowering and seed production of all three (per individual). The gentian does not appear to have good "flowering-years" on the fell as the other species do. It maintains a small, regular input into flowering. Unlike the other two species, flowers are cross-pollinated, this mechanism probably serving to maintain a high level of genetic variability, at little cost to the resources of the plant, and in this way enable adaptation to changes in selection pressures.

Gibbons (in prep.) considers that flowering in *Gentiana verna* is at a selective disadvantage under conditions on the fell-top compared with a site at Langdon Beck, Teesdale (386 m), where the mean flowering percentage is somewhat higher.

In the study area greater than 90% of the individuals in the Gentiana verna population do not enter into the sexually reproducing phase each year. The energy expenditure of flower, fruit and seed production is thus avoided. The ramets which this species produces have no high initial mortality risk and in this respect are comparable to the newly emerged seedlings of Polygala amarella. The gentian, however, in producing vegetative recruits also avoids the wastage of energy which takes place when seeds are lost before germination and in this respect is energetically more conservative than Polygala. The gentian is genetically more conservative, too. Vegetative reproduction maintains a tested genotype as the functional unit of the population.

In the three species a range of strategies for the production of new individuals is apparent. Draba is the most R-adapted and gentian the most S-adapted. The lack of a seed-bank in the two sexually reproducing species fits well with the trend outlined in a review by Thompson (in press) of the occurrence of seed-banks along environmental gradients of stress and disturbance.

All three have a genetically and energetically conservative modes of reproduction, fairly low flowering percentages being common to all three species, as are protracted juvenile stages. The latter is less significant in the gentian.

Though variations exist between the reproductive strategies of the three, their overall mode of reproduction seems to correspond closely with what would be expected in stress-tolerant plants.

11. SURVIVAL AND GROWTH

As a plant grows the competitive interaction between it and surrounding vegetation increases. Competition for light, water and mineral nutrients may result in the death of the individual or a variety of plastic growth responses. Various accounts of behaviour of the population at this level are present in the literature and the species of this study must be considered in the light of what is known about phenotypic plasticity in plants.

Alteration of rates of growth and the resultant distribution of size classes in the population has been used to predict future population trends in teasel to great effect.[108] The authors note that this approach would be of greater significance in plants with very plastic morphology.

Other effects of stress are well-known to horticulturalists. Plants which are deprived of mineral nutrients or water will often channel resources from vegetative parts into flower production and thereby flower much earlier than would otherwise be expected.

The existence of intra-specific variability in energy allocated to reproductive structures has been demonstrated and linked with environmental gradients. Gadgil and Solbrig[26] found greater partitioning of resources into seed production in biotypes of Taraxacum from open, disturbed habitats. The evidence supported the r-K theory, and can now be used as an example of R-adaptation.

Hickman,[43] considering evidence for environmentally mediated plasticity in resource allocation in four species of Polygonum, warned against incautious application of the r-K theory. He states that the pattern of energy allocation in Polygonum kelloggii is the opposite of that predicted by the r-K theory: "the most energy is allocated to seeds in the environment that remains moist the longest and has the greater plant cover".

This pattern does not contradict the C-S-R theory, however, since greater resource partitioning to seeds would be expected as a response either to competition directly or to stress as it results from the sequestration of mineral nutrients by already established plants. In both these cases larger seed would be favoured.

The area of energy allocation and plastic growth response has not been studied in the species of this study. All that can be done in this section is to attempt to evaluate what is basically anecdotal evidence on the variability of growth and form in *Draba*, *Polygala* and *Gentiana*.

The existence of a protracted juvenile stage in *Draba* and *Polygala* has been noted.[9,10] The authors consider that the advantage to the plants is that a large cohort establishing in one year, due to good seed-set or favourable conditions for germination will produce flowers over a succession of years, thereby increasing the chance of encountering another favourable year when good seedling establishment would again be possible. Time of onset of flowering is an expression in the mature plant of post-germination variability in growth noted in the last chapter. [illegible]

As discussed in section 3.1 the species of this study were chosen primarily for their lack of plasticity. There are two instances, however, when a certain amount of variability in structure becomes apparent. Both occur as a response to grazing damage in *Polygala* and *Draba*, but have not been observed in the gentian.

The first is a response of the juvenile plant. When some, or all, of the leaves are removed, some plants will exist for a period as a rootstock only, with no visible rosette. These are very difficult to identify in the field and must often go unnoticed in this form. The first sign visible to the observer subsequently is of one or more tiny rosettes growing from the old rootstock. These grow as far as can be ascertained from observation, in exactly the same way as a juvenile plant. Hence, the old plant is rejuvenated by this process. The new rosette has the appearance of a young plant in its leaf morphology and presumably undergoes the same cycle of growth and senescence as a newly established plant. It has, however, an already-developed root system.

In Draba a similar process has been observed when immature inflorescences are removed by grazing. This prevents the death of the plant which would be the normal consequence of flowering and fruiting. Plants damaged in this way have been observed to flower and die in the normal way in subsequent years.

The second response to damage is that of the flowering plant. This has already been mentioned in section 8.3. Little now needs to be added, except that this process, promoting as it does increased vegetative and reproductive growth may also increase the vigour of the plant. In the case of Polygala, which continues flowering for several years, the existence of several rosettes on one rootstock will probably increase the chances of at least one surviving the grazing pressure and thereby increase the longevity of the individual as defined in this study.

Individuals of Draba incana grown in the lab have been observed to produce subsidiary rosettes on stolon-like structures arising from axillary buds. The morphology of plants grown in the laboratory is very different from those found on the fell, however, and it would be unwise to conclude that this process occurs in the natural situation. Rosettes produced in this way have not been observed to become separately rooted individuals.

Tamm[97] has noted that the orchids of his study may adopt a subterranean life for one or more years, existing by a mycorrhizal association similar to that which is common among juvenile orchids before leaves are produced.

By such means it is possible that some individuals, avoiding the hazards of bearing a well-developed aerial shoot, increase their life expectancy to some extent. In particular, those individuals of Draba and Polygala which produce new rosettes on an old rootstock have the advantage of an already developed root system.

To what extent these species have established adapted biotypes throughout their range in upper Teesdale remains unknown. The differences in seed production between the Cronkley and Widdybank Fell populations of Draba incana might prove an enlightening avenue for further study.

Results on the flowering behaviour of the three species, being of a fairly descriptive nature, need little amplification here.

In order to incorporate a discussion of the flowering strategy of each of the three species into an explanation on their overall adaptive strategy, results of the form obtained by Hickman[43] would be necessary. In addition, some measure of the resources which the gentian partitions into the production of new ramets would be invaluable. However, these results are almost impossible to obtain from the species in question due to their rarity, and clearly extrapolations cannot be made from garden experiments since this environment is certain to affect resource partitioning.

Behaviour of the type noted in this section requires a more sensitive means of describing the individual. However, in the study populations these most extreme forms of morphological plasticity only occurred in a very small percentage of the population. The extent to which Harper and White's[38] more sensitive symbolism (see section 9.1) is necessary depends on the frequency with which such variability is observed in the population and its magnitude. It is not felt that the overall description of the dynamics of the study populations presented here would have benefitted from such an approach, though it is probably appropriate to the violets studied by Doody[21] which have a much more complex growth form than any of the species of this study.

12. MORTALITY PATTERNS AND AGE-STRUCTURE

As Harper[36] notes, very few long-term studies have been carried out on perennial plant populations. Those which have been published since the appearance of his "A Darwinian approach to plant ecology"[35] have tended to assume that populations of perennial plants decay in a manner analagous to radio-isotopes, that is, independent of age, resulting in depletion or survivorship curves with a negative exponential form. Harper has summarized much of the recent work in "The Population Biology of Plants".[36]

Given the undoubted plasticity of plant form, especially as a response to environmental constraints and competition, it seems somewhat surprising that plants should decay in this manner. If, as Harper[36] suggests in connection with seasonal mortality rhythms, there is a greater risk of death when plants are growing fastest, it seems reasonable to assume that mortality would be greatest at those periods in the life-cycle when plants grow fastest. This has been demonstrated, as noted in earlier sections, with seedlings and seems to be a likely consequence of flowering in mature plants. For those species of plants which flower at a given period in their life-cycle, and in which flowering is associated with rapid tissue growth, it might be expected that an age-dependent effect in mortality would be apparent. If the latter is true, then for those plant species which become particularly vulnerable to predation due to the production of inflorescences, as the species of this study do, a greater effect would be expected.

One of the failings of the negative exponential model is of its complete rigidity in ascribing mortality risk as a function of number in the population only. The mechanism from which constant annual mortality results has not been explained.

Hett and Loucks[42] summarize their objections to the negative exponential model when applied to tree species, thus:

> "Intuitively, one expects that as an individual grows from an understorey position into the canopy, the environmental stresses change. As one example, interception of light will increase, decreasing the probability of mortality due to shading. Thus, a model which includes provision for a changing mortality rate ... should be expected to provide a better description of population depletion over long periods of time."

In raising these objections to the negative exponential model of plant mortality it is sought to examine the shortcomings which have resulted from its application to plant demography studies, some of which have not provided data adequate for testing against the model.

When Deevey[19] described three overall shapes for survivorship curves found in the animal kingdom, one of his most striking discoveries was the existence of exponential decay in many bird species, a finding which has been upheld by recent studies (see references in Coulson and Wooller).[18] Deevey (op. cit.) cited Lack's observation that mortality rates estimated from the latter's data were not likely to be reliable beyond the fourth or fifth year due to lessening sample size. The studies from which these results were taken had been carried out over periods of up to twelve years. Studies on plants have seldom been carried out over a time-scale as long as this, and it is essential to consider the period of study in relation to the lifespan of those individuals being studied if meaningful conclusions are to be drawn.

It is instructive to examine results in the literature and from the present study bearing these criticisms in mind.

The survivorship curves of winter annuals have been described[61,106] and found to be strongly negatively skewed, corresponding to Deevey type I. In Cerastium atrovirens[61] greatest mortality occurred at the time of seed maturation in May. This would be when competition was greatest with the surrounding vegetation. The peak of mortality discovered during inflorescence development in *Vulpia fasciculata*[106] was thought to have several causes: desiccation, shading and the grazing of developing inflorescences by rabbits.

Strongly positively skewed growth curves have also been demonstrated in annuals. Sharitz and McCormick described the population dynamics of *Sedum smallii* and *Minuartia uniflora*.[88] The time of seed formation was the initial point on their survivorship curves, and they commented that positive skewing was likely to arise as a consequence of including the earliest stages in the life-history on a survivorship curve.

Annuals have a well-defined mortality pattern and a fairly short period of observation is sufficient to adequately describe it.

Perennial plants, on the other hand, require a longer period of study in order to be able to describe adequately the mortality patterns which characterise them.

The negative exponential decay of those species described by Tamm in 1956 seems conclusively proved. These plants were recorded over a period when management practices on the grassland remained constant. The gentian of this study, which shows great conformity with the negative exponential model, grows in the most stable vegetation type in upper Teesdale. This vegetation type, as far as can be judged, is grazed to the same extent each year.

It might be reasonable to predict that exponential decay would result in those habitats where selection pressures are constant. In his 1972 paper, Tamm draws attention to the irregularities of the orchid species he studied compared with those of the 1956 study, and suggests that the changes in management practices were the cause.

Harper[36] interprets Tamm's findings, thus: "The linear depletion curves observed for other species are not found with the orchids over the whole period, though episodes of exponential decline can be recognised".

Episodes of exponential decline cannot be taken as predictors of a general trend. Several papers have been published recently recording exponential decline in a variety of species. These include three species of Ranunculus (see section 6.3), Mercurialis perennis[48] and two species of Plantago.[40] As the duration of the study period decreases, the relative importance of fluctuations in the survivorship curves due to seasonal effects increases. The overall shape of the survivorship curve described will be influenced by the time of year at which the study commenced and the seasonal periodicity in mortality, quite apart from any effects due to the age of the population itself. Exponential decay is of any real significance only if it is demonstrated in a long run of annual samples within a cohort or mixed-age population.

On considering evidence in the present study and in the literature, what generalizations can be made about the form of survivorship curves of perennial plants? The conditions which seem to favour exponential decline have been described. Plants survive or die in intimate contact with the surrounding plant and animal community. Autecological studies of the type described here focus attention on what may be best regarded as a monitor of changes taking place in the vegetation as a whole. The sum total of the life strategy of a single species represents the overall adaptation to its environment. In perennial plants, those individuals that die represent the 'failures'. Individuals 'fail' in response to selection pressures in the environment. It is not unreasonable to look to the environment of the plant to identify the mechanisms from which mortality patterns result.

It has been stated that exponential decline is most often seen in constant environments. One imagines a constant group of selection pressures resulting, in the case of the gentian in this study, from inter-specific competition from the plants with which the gentian grows, modified to some extent by the grazing of sheep. The number of niches, or "safe-sites", which are available to immature gentian plants is almost certainly greater than the number available to larger, mature rosettes. The exponential survivorship curve may relate to the survival of the niche as a suitable site for the gentian. As individuals grow they compete more vigorously with their neighbours, they prevail or die. It is likely that a far greater number of "safe-sites" exist within the sugar limestone grassland for young gentian plants than for old, mature individuals which also tend to be larger. The survivorship curve is best considered as a function of the selection pressure operating within the environment.

In contrast to the gentian, Polygala amarella and Draba incana live in more unpredictable niches. In the case of Polygala this results from the production of a long inflorescence and thus being elevated to a height where grazing damage is more likely to affect, not just flowering, but the vegetative growth of the plant (see section 8.2). Draba grows on open, eroding sugar-limestone and on ephemeral bare patches in the limestone grassland turf. It is very sensitive to competition. Selection pressures therefore have a physical and a biotic component.

Both these plants develop a woody rootstock, from which new rosettes can grow if already mature leaves are removed. The development of woody tissue has not been observed in the gentian. It is possible that the early development of a strong root-system is an advantage to certain individuals of Draba and Polygala. In Draba this can be visualized as a stabilizing mechanism in unstable soils, permitting deep root growth into lower levels where moisture is likely to be more freely available. Polygala grows on more mature soils than Draba, the main purpose the woody rootstock serves in this case is to anchor the rosette against the force exerted by grazing animals.

In both these species survivorship curves are characteristically steeper in the early stages and have a long "tail". It is probable that the greater tenacity of a small, though significant, number of older plants is due to the development of woody tissue. Since Hett[41] and Hett and Loucks[42] have discovered a similar effect in several tree species, it could be that the occurrence of a survivorship curve in which mortality rate decreases with age occurs as a result of wood growth. Hett and Loucks (quoted earlier) describe a scenario in which a power-function model would be expected to provide a better fit than negative exponential. Similar arguments have been used for Draba and Polygala, seeking to relate the growth habit of the individual to the particular environmental stresses which it experiences.

The ability to go on producing new aerial rosettes from an already-established rootstock fits well with the theory that the plants of this study are adapted to stress. The existence of a persistant organ from which new rosettes grow would be at a high selective advantage in an environment characterized by low annual productivity, since this would obviate the necessity to renew root-growth each year. Genotypes with strong root development would be expected to be at a selective advantage under the conditions in upper Teesdale.

A consequence of this would be that older plants tend to make up a greater than expected part of the population. Consideration of figure 7.2.a shows that this is indeed the case. By 1977 the three and four year old age-classes of Draba incana had died out, as had the four and five year old age-classes of Polygala amarella on Widdybank Fell. These populations, and that of Polygala on Cronkley to a less marked extent, have undergone a period of decline, presumably due to consistent adverse selection pressures, and this has resulted in a bias towards young and old plants in the population. Higher numbers of younger plants are expected due to continuing recruitment, albeit at a low level. Old plants are expected to be at selective advantage under these conditions also, for reasons outlined earlier. Hence, observed changes in the age-structure of the study populations of Polygala amarella and Draba incana seem to support the hypothesis of greater tenacity in older plants, that is, of decreasing risk of mortality with age.

Due to the overall plasticity of plant form, age-structure will never come to occupy the central role in plant demography which it does in animal population dynamics. Harper,[36] citing the work of Uranov and Smirnova[103] and Uranov et al.,[104] who along with Rabotnov,[78] have developed a system of classifying plants not by age, but by "life-states" dependent on factors such as size and maturity, suggests that elements of age-structure or "stage-structure"[108] investigations would be at their most powerful when used together. Werner and Caswell[108] found significant age-dependence in mortality of large rosettes of teasel of age greater than five years, thus Harper's prediction is borne-out.

Since various rejuvenation processes take place in plants, "stage-structure" analysis would seem to be more appropriate to the study of the population dynamics of perennial plants. This conclusion, and the importance of the work of Werner and Caswell (op. cit.) should be borne in mind when plant demography studies are in the planning stage.

13. CONCLUSION

Plant demography, when compared to that of animal populations, is still in its infancy. Problems which Harper indicated in "A Darwinian approach to plant ecology" ten years ago are only now being unravelled.

Evidence presented in this study allows examination of the theory of exponential decay in plant populations and indicates that the plasticity of the individual and stage-structure analysis might yield far-reaching results.

In terms of the adaptive strategies of the three species studied, all appear to show adaptations at every stage in the life-history which are best understood as responses to a stressed environment.

Hopefully, the results will be of use to conservationists seeking the best returns for effort in ensuring the continued existence of the rarities. The probable absence of a seed-bank for Draba incana and Polygala amarella is important in this respect, as is the likelihood that certain individuals have considerably greater longevity than the majority of the plants in the population. These long-lived individuals may impart some long-term stability to the populations, but in order to assess their full importance to conservation, their contribution to the intrinsic rate of increase of the population must be known persistent, though non-reproductive individuals being of little benefit to the continuance of the species.

Return for effort is a problem which plant demographers must consider. If information had been collected on the vigour of these Teesdale plants and analysed in conjunction with age-classes conclusive results on age/stage dependence in mortality may have been demonstrated. What is certain is that far fewer individuals and less species would have been studied since the effort on each would have been greatly increased.

Plant demographers are now in a far better position to frame the questions which they are attempting to answer in studying the demography of perennial plants than they were ten years ago. Hopefully, the results of this study may go some little way to aiding them.

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ADDENDUM

These sections were prepared, post-examination, to include a valuable reference* hitherto overlooked by me. I am grateful to my external examiner, Professor John Harper of the School of Plant Biology, University College of North Wales, Bangor, for drawing it to my attention and for other helpful comments and suggestions on the thesis. Certain of the latter are included in section 1 of this addendum.

Section 1

This relates to sections 3.1 and 9.1 of the thesis.

It should be noted that individuals of Draba and Polygala are genets, whilst those of Gentiana are ramets, or units of clonal growth. Since natural selection operates on the whole life-cycle, from zygote to zygote, the individuals described do not form analogous starting points for natural selection.

Strategies described in the thesis relate to the replication of the individuals as defined in section 3.1. Terms "life-cycle strategy" and "adaptive strategy" relate solely to this process and are synonymous in the body of the text. It is in this sense that the descriptive data on demography are presented. Comments on the evolutionary significance of these data are conjectural and it should be remembered that the evolutionary consequences of natural selection are expressed only by genets.

Section 2

This relates to section 4.3 and figure 4.3.a; and section 6.3., figures 6.3.a. I-IV.

4.3 (revision) Mortality of Draba recruits in first six months.

Survivorship curves of recruits of Draba incana have been re-drawn on a semi-logarithmic graph, following the recommendations of Williamson*. The relative changes in the numbers in the cohorts may now be seen. Only in this form do steeper sections of the curve indicate a greater mortality rate.

No constant pattern of mortality is visible on the graphs, so no conclusions may be drawn from them alone.

The survivorship data for these cohorts have been analysed in a similar way to those of Polygala and Gentiana (Table 4.3.a., page 42). This table may be found on page 3 of this addendum.

The figures from six out of the nine cohorts have a greater mortality during the first interval than the second (+). There is, therefore, some indication that mortality of Draba plants is concentrated in the youngest stages.

	Year	Plot	Original number	First Interval(days)	Survivors	Mortality	Second Interval (days)	Survivors	Mortality
	1971	5:3	97	65	74	0.2371	106	10	0.8649
+	1972	5:3	46	84	23	0.5000	54	13	0.4348
+	1970	2:1	229	56	144	0.3712	100	131	0.0903
+	1971	2:1	77	69	47	0.3896	85	33	0.2979
	1972	2:1	179	84	136	0.2402	58	85	0.3750
+	1973	2:1	40	89	18	0.5500	42	13	0.2778
+	1970	8:1	159	53	102	0.3585	105	68	0.3333
+	1971	8:1	53	71	30	0.4340	107	19	0.3667
	1972	8:1	288	83	143	0.3667	61	74	0.4825

Figure 4.3.a. : Survivorship curves of *Draba* recruits
I plot 5 : 3 and 8 : 1

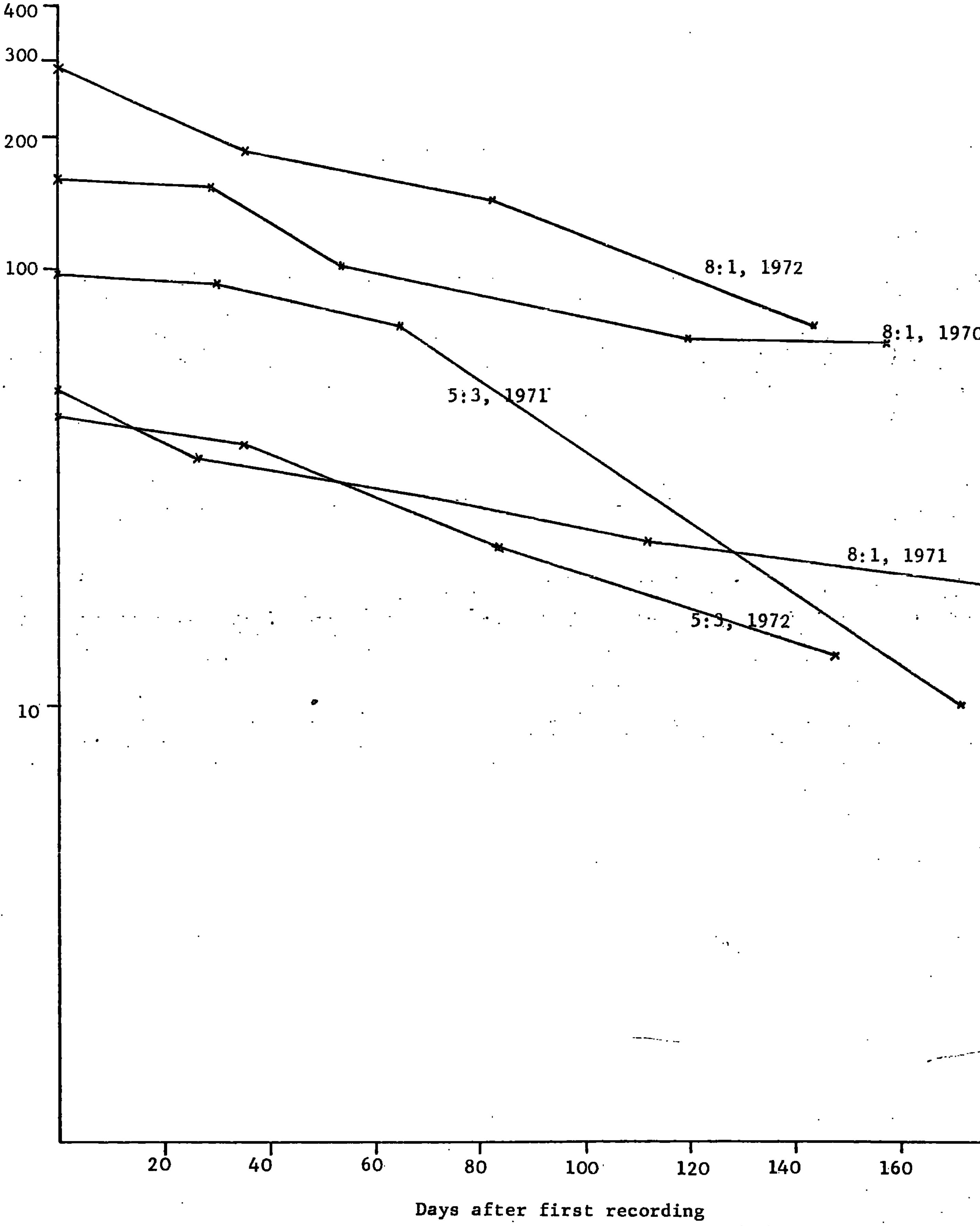
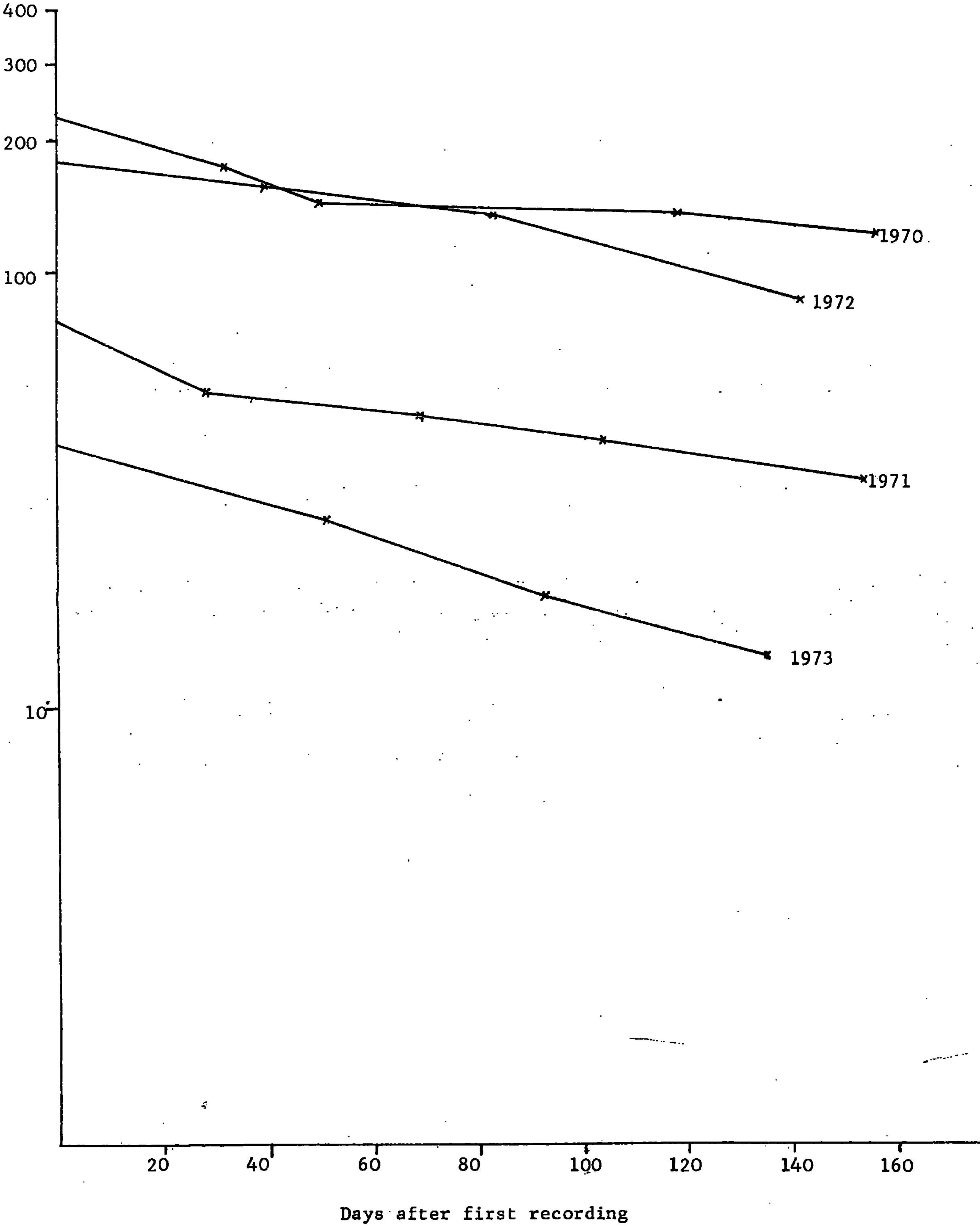


Figure 4.3.a. (cont.) : Survivorship curves of Draba recruits.
II plot 2:1.



Section 6.3 (revision)

The data have been re-exposed as semi-logarithmic graphs*. The depletion curves of the original mixed-age population (DC) and survivorship curves (SC) of the cohorts are shown on the same graph, as before.

Depletion and survivorship curves of Gentiana verna are transformed by this treatment into almost parallel lines, indicating constant annual mortality in that part of the population represented. Since these curves are representative of the population as a whole, one may conclude that established plants decay exponentially.

Populations of Polygala and Draba behave differently. As expected from the consistent pattern of deviation from expectation calculated using the likelihood ratio test, these curves do not transform into straight lines when numbers are expressed on a log scale. As noted on page 61 certain of the cohorts exhibit this tendency to a greater degree than others. The effect is visually most apparent in the plots of Polygala amarella from Cronkley Fell. The statistical analysis of this phenomenon is explained in the text.

* Reference: WILLIAMSON, M. (1972) The Analysis of Biological Populations Edward Arnold, London.

Figure 6.3.a.I.: Depletion and survivorship curves of Gentiana verna

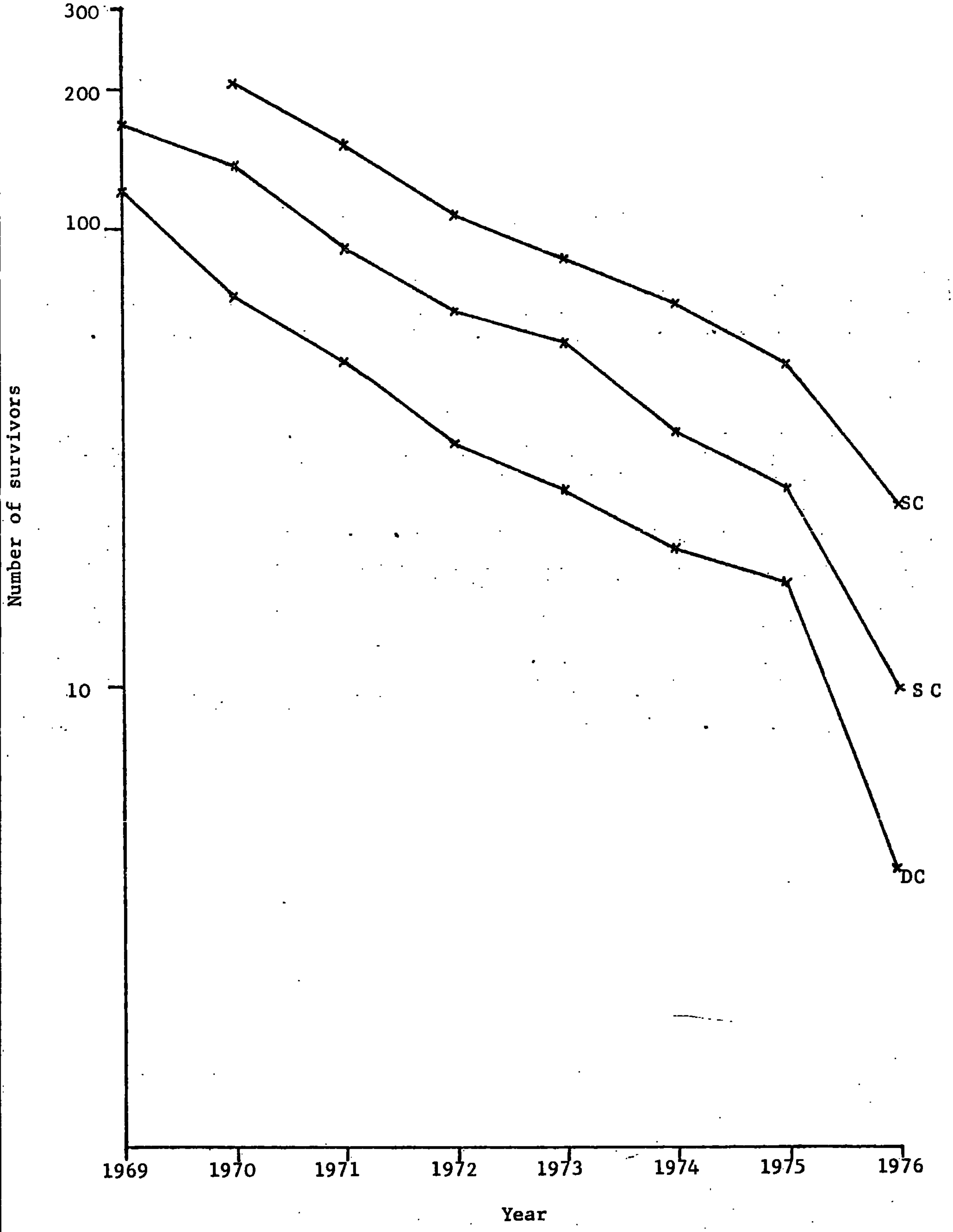


Figure 6.3.a.II : Depletion and survivorship curves of *Draba incana.*
(N.B. No record for 1975 on survivorship curves)

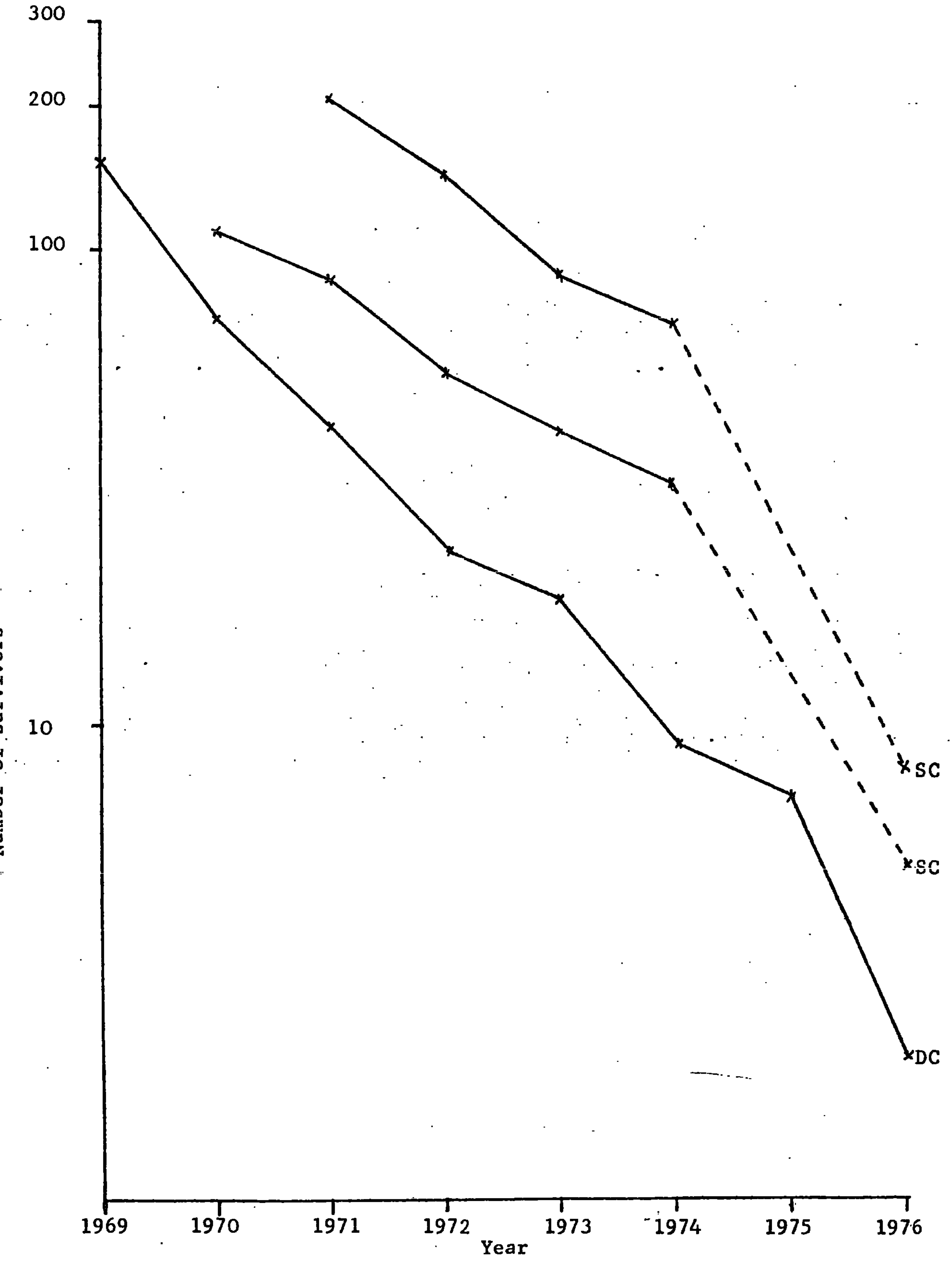


Figure 6.3.a.III : Depletion and survivorship curves of *Polygala amarella* on Widdybank Fell.

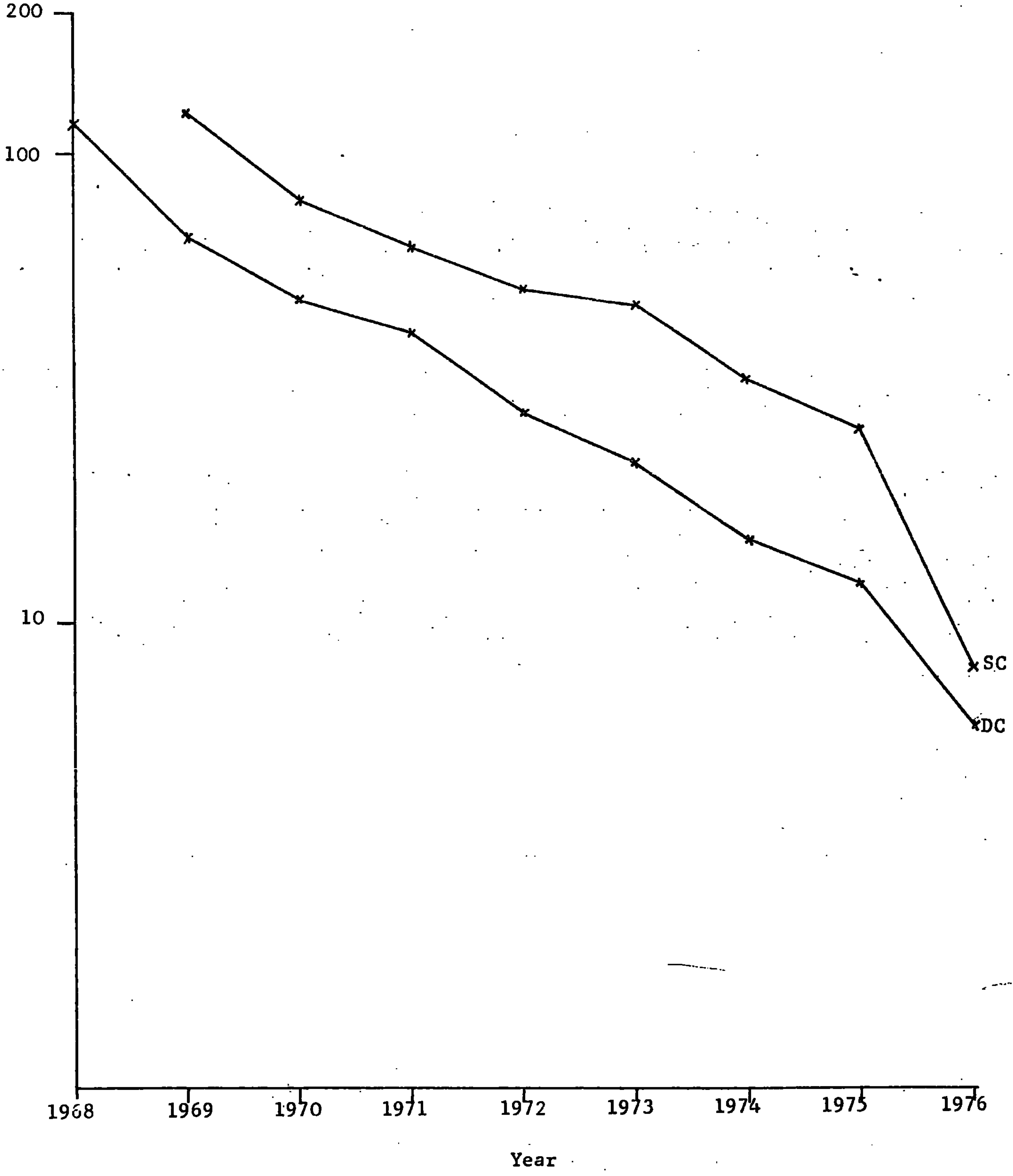


Figure 6.3.a.IV : Depletion and survivorship curves of *Polygala amarella* on Cronkley Fell