Studies in the Autecology of Juncus Squarrosus L

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Studies in the Autecology of *Juncus squarrosus* L.

thesis presented for the degree of M.Sc. in the University of Durham

by

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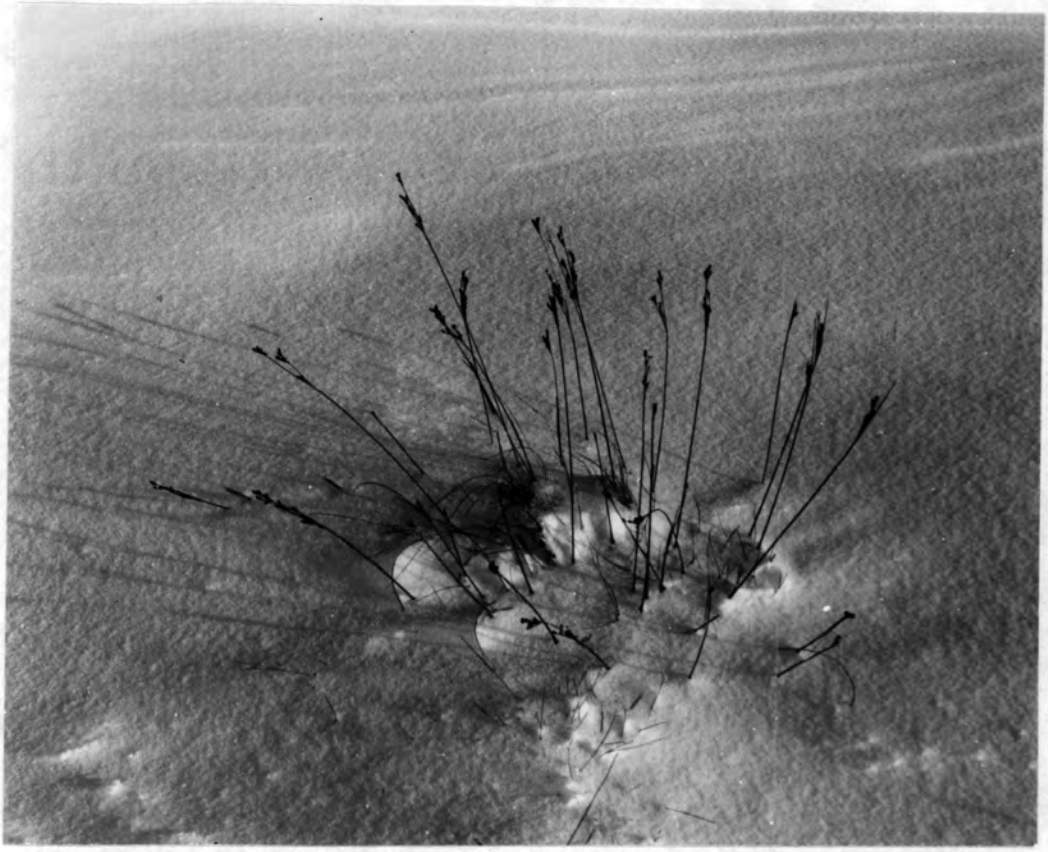

Plate 1 - Frontispiece: Inflorescences in snow.

ABSTRACT

Studies in the autecology of *Juncus squarrosus* L. have been made over a three-year period, mainly in the area of high-level moorland at the head of Teesdale in the north Pennines.

The morphology and anatomy of the plant are described, and an account is given of the form of the communities. Annual increments in rhizome growth of 0.5 to 2.0 cm. were recorded.

About 20 sites were examined phytosociologically. Five noda were distinguished, namely the peaty gley, the podsol, the species-poor gley, the species-rich gley and the flushed-peat noda. The reproductive capacity was measured at 12 of these sites. Where *Juncus* is dominant up to 8,000 seeds can be produced per square metre. Production is lower on well-drained soils, the number of florets per inflorescence being less, and when a smaller proportion of florets ripen to form capsules. In average years 50% of the florets ripen at heights up to 1800 ft. (550 m.). Larvae of the moth *Coleophora alticolella* eat the seeds at the lower levels, and changes in its population size have been followed.

Seed viability is usually high, but experiments showed that germination requires light at the normal field temperatures. Seedling establishment was found to be uncommon, though large numbers of dormant viable seeds are present in the soil.

Various observations are described which provide information on the ecology of *Juncus squarrosus*. Sheep grazing is held responsible

for its present widespread occurrence, and a slow spread will continue in certain of the better grasslands if the grazing pressure is maintained. But this cannot be considered a serious threat to the value of the uplands as the plant has some nutritional value, and most stands contain a considerable proportion of grass. Callunetum, the climax vegetation, is of less value agronomically in the area studied.

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I wish to thank the gardening and technical staff of the Department of Botany in Durham for help in various ways, especially Mr. Redhead for the photocopying of my tables, figures and plates. Mr. T. Peabody gave valuable help by regularly counting the number of seedlings in my germination experiments. Miss J. Wheatley typed the thesis, and Messrs. G. Bailes and Sons have done the binding.

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SECTION I: INTRODUCTION

Juncus squarrosus is a plant mentioned frequently in the literature, but there has been no attempt to draw the information together into an autecological account previous to this thesis. The genus as a whole, and several of the species have been described in the Biological Flora of the British Isles by Richards and Clapham (1941 and 1943). Pearsall also, has gathered information on *Juncus squarrosus*, and gave a short paper at a British Ecological Society meeting in 1949, besides incorporating much into the New Naturalist volume, Mountains and Moorlands, 1950.

According to Clarke (1900), the first record of the species in Britain is given in Parkinson's Herball of 1640 - 'on a high hill in Wales called Bewrin, in sundry wet and moorish groundes in many places thereabouts'. The name is that given by Linnaeus in the Species Plantarum (Edition I, p. 327), and has been in use ever since. Moor rush is the current English name for the plant, but stool-bent is usual in farming literature, and Winch in 1805 gave goose corn and moss rush.

Taxonomically, *Juncus squarrosus* is near-constant in its characters throughout its whole range, though varying in size according to habitat, and it is sharply distinct from other rushes. The only variety that I have discovered in the literature, and after searching through herbarium material in the British Museum, is one with long flaccid leaves, and pale perianth segments. This was recorded by Hubbard and Sandwith (1928) as a new species (Juncus ellmanii Hubbard, Sandwith and Turrill) from Spain, but similar plants have been collected also from Bampton in Westmorland and Foss in Perthshire. On re-examining the Bampton locality, I found abundant Juncus squarrosus, but all was of the normal form. Löve and Löve reported (1948) a chromosome number of 2n=40, as in Juncus acutiflorus, conglomeratus and effusus, and this has been confirmed subsequently.

Juncus squarrosus is found in most of Europe, having an Atlantic distribution. It extends south to the Alps and the mountains of S. Spain, with an isolated occurrence in Morocco, and east to the Dnieper in W. Russia. It occurs as far north as S. Greenland, and is also found in Iceland and Scandinavia, especially in the western oceanic areas.

Though recorded from 109 of the 112 vice-counties of Britain, and all 40 Irish vice-counties (Clapham, Tutin and Warburg, 1962), the species is abundant only in northern and western Britain and Ireland, as shown by the distribution map in the Atlas of the British Flora (1962). In S. E. Britain it is confined to areas of strongly acidic soil, e.g. the Weald clays and sands, and the Bagshot sands of the New Forest. There is no altitudinal limit to its range in Britain, as it is found up to the tops of the highest mountains wherever soil conditions are suitable. It occurs plentifully in rough grasslands, moors and bogs, being the dominant species in some communities, though scarce in others. These three vegetations are together classed as rough grazings, which in 1954 were estimated by the Natural Resources (Technical) Committee to amount to 16,200,000 acres (6,556,000 ha) in England, Scotland and Wales. As this is over one third of the total area of land available to agriculture in Britain, it is clear that Juncus squarrosus is of considerable importance to the agriculturalist.

To understand fully the interrelations of the constituent plants and animals of these communities, and how the communities themselves interact, it is necessary to know the autecology of the more important species present. The work described in this thesis will help to answer such questions as:- Why is Juncus squarrosus present on that hill slope but not this? Is Juncus squarrosus likely to spread here? What function has Juncus squarrosus in this ecosystem? Is it of benefit to man for Juncus squarrosus to grow there? Full answers are not possible till the autecology of the other species is known, and synecological work has been done on how they compete with, assist, or provide food for each other. But a knowledge of the life processes of the plant goes a long way towards explaining its distribution, status and potential in our rough grazings.

Most of the work described in the thesis has been done in the area of high moorland at the head of Teesdale in the N.

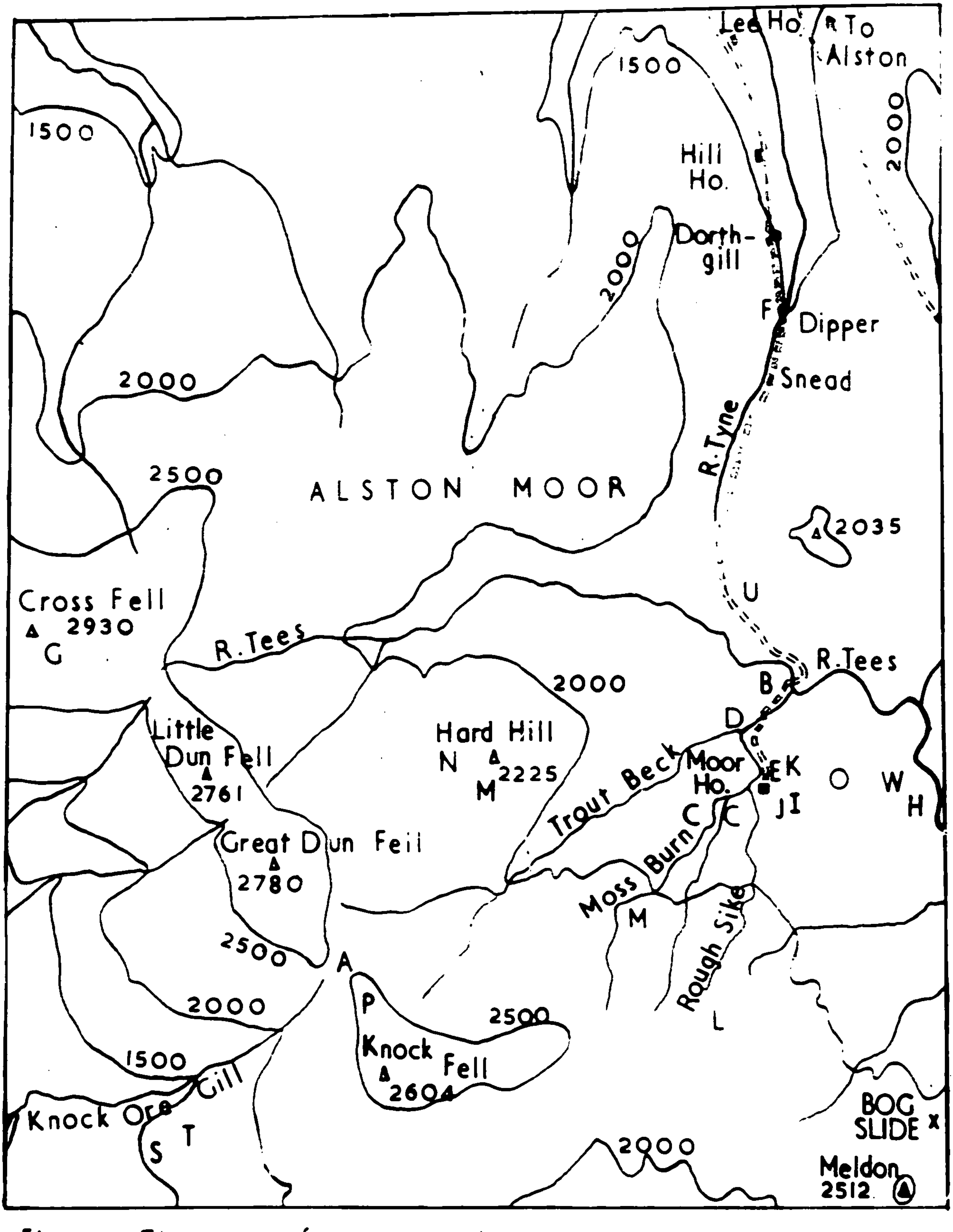


Fig 1.1. The area of study, showing sampling sites, streams, contours and roads. Heights in feet.

Pennines, chiefly in the Moor House National Nature Reserve, which is in N. E. Westmorland to the south of the river, and which also extends down the western escarpment of the fells. A map of the area is given in Fig. 1.1. A considerable amount of research has been done on the Reserve, giving rise to many publications, with the result that there is a good background knowledge to the environment.

The climate is severe, having been described by Manley (1943) as broadly resembling that of S. Iceland, with strong winds, low summer maximum temperatures, frosts in any month, and long periods of snow-lie in winter. Recent 10-year averages (Millar, 1964) for the Moor House meteorological station at 1840 ft. (560 m.) O.D. are :- yearly mean temperature 41.5°F. (5.3°C.), mean of warmest month, July 51.9°F. (11.1°C.), rainfall 74 in. (1877 mm.) and snow cover 55 days.

The geology of the area has been described in a monograph by Johnson and Dunham (1963). Most of the rocks belong to the Yoredale Series of the Carboniferous, giving sandstone, shale and limestone outcrops, and are usually covered in glacial clay. Thus there is a variety of soil types, and with a range of altitude from about 1,000 ft. (305 m.) to 2,930 ft. (893 m.) on the summit of Cross Fell, this gives rise to a range of *Juncus squarrosus* communities fairly representative of those in all Britain.

Cragg (1961) summarises work on invertebrate population numbers by zoologists who have taken *Juncus squarrosus* as one community type. Studies on the Tineoid moth *Coleophora alticolella* Zell. are particularly relevant to the autecology of *Juncus squarrosus*. Among the botanical work has been a report (Welch and Rawes, 1964) on the changes following the exclusion of sheep from upland grasslands including a *Juncus squarrosus* community. Thus the thesis fits into the general pattern of research done at Moor House into upland land-use, and process in upland communities, and has been helped by results already available.

Apart from the introduction and the concluding discussion and summary, the material in the thesis has been divided into six sections, each concerned with a particular subject. Each section has been given its own paging, with the section number prefixed; this has also been done with tables and figures.

Following this introduction, numbered as section 1, there is a short second section describing the morphology and anatomy of the plant. A longer third section is concerned with reproductive capacity, and includes information about seed dispersion and viability. Germination and the factors controlling it are the subjects of section 4, while section 5 gives an account of the establishment of the seedlings and the growth forms of the plant. A full description of the communities in which *Juncus squarrosus* is found follows in the next section on phytosociology.

In section 7, the ecology of Juncus squarrosus is described, and its value discussed. In recent literature, it has been said that Juncus squarrosus is spreading in the British uplands because of poor grazing management, especially overgrazing, and that this is detrimental to the quality of the grazings. These statements, which were a stimulus to making the study, are examined and further defined.

Finally, in section 8 there is a brief summary and full bibliography.

SECTION II: MORPHOLOGY AND ANATOMY.

A) Morphology

The morphology of the rhizome and roots of *Juncus squarrosus* is well described by Heath and Luckwill (1938).

A dense covering of old leaf bases conceals the sympodially branched rhizome, which grows horizontally at a depth of about 2 cm., much of this being due to the litter of its own leaves. The rhizome growth follows a forward expansion of the shoots - there is no penetration of the soil by the terminal bud of the rhizome. The annual growth increment is between 1 and 2 cm., depending on the soil and the amount of competition from other species. The rhizome is from 6-12 mm. in diameter. It twists, since the terminal bud of the front shoot which produces the rhizome forms the inflorescence, and growth is continued by one or more lateral buds.

The roots are of the cord type, at first white, but becoming light brown with a wrinkled surface later in the season. They tend to grow vertically downwards, with little lateral spread. They probably die after a year, but remain in the soil functioning as a holdfast for several more years. Most roots are within the top 10 cm. of the substratum, Heath and Luckwill giving a working depth of 2.5-9 cm., and a maximum depth of 27 cm.; this agrees well with my observations at Moor House. Short lateral rootlets occur sparingly on the

Plate 2 - Section 2: <u>Juncus squarrosus</u> rosettes in a sward.

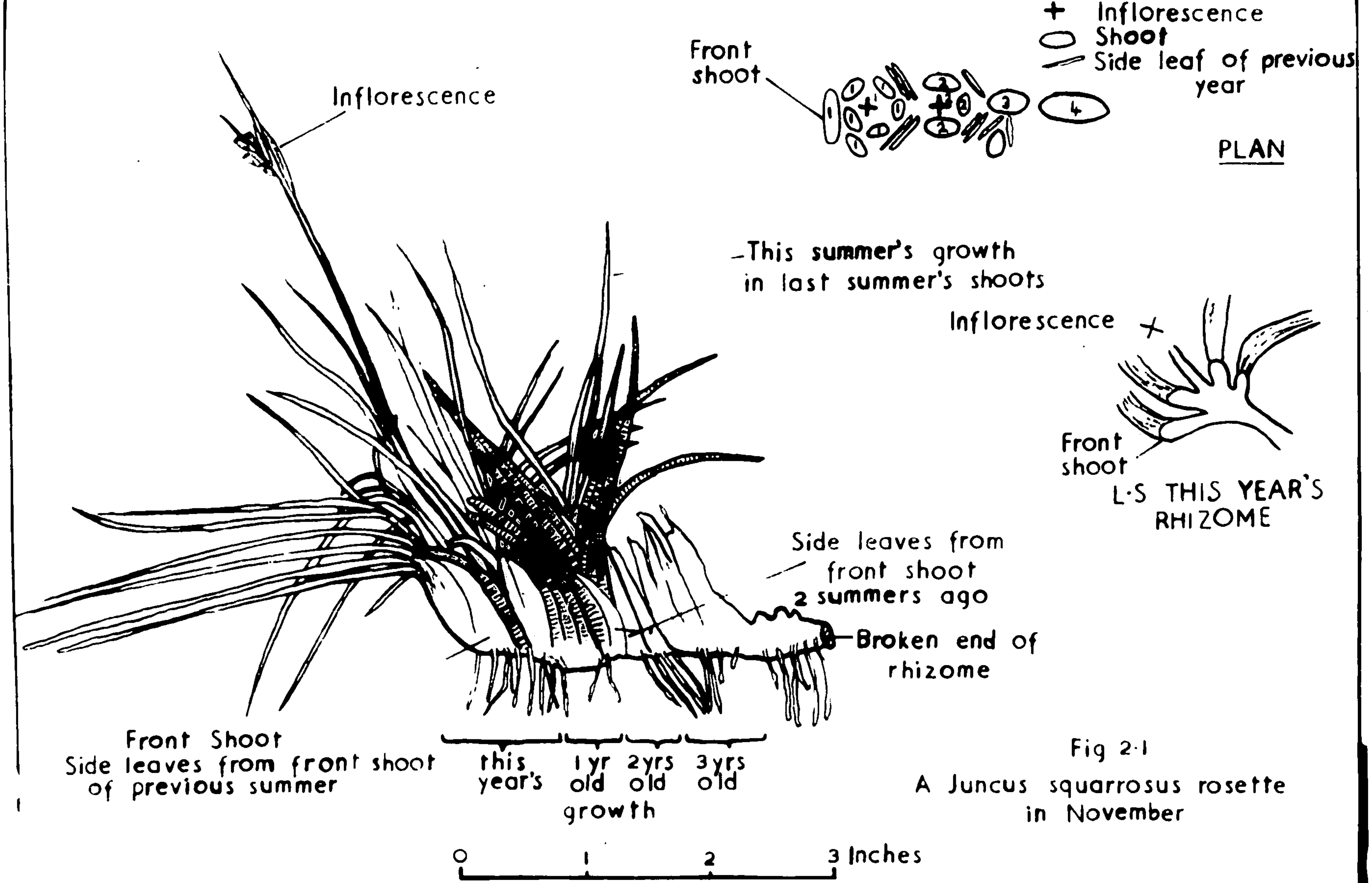


Fig 2·1
A Juncus squarrosus rosette in November

younger cord roots, and root hairs 1 - 3 mm. long form a dense weft (though sparser in very wet conditons) around the roots, which are 2 - 3 mm. in diameter when mature.

The leaves are radical, except for one subtending the inflorescence, and are borne in several shoots which together form the rosettes. (It must be mentioned that Kershaw and Tallis (1958) use shoot in the different sense of describing all the growth initiated in one year). In favourable places, where there is also rank growth of other species, e.g. wet flushed peat, the leaves may reach a length of 25 cm., but they are mainly 5 - 15 cm. long. They usually reflex sharply above the sheathing base, and tend to grow out above the surrounding turf, as shown in Plate 2, but where growth is dense, the leaves are forced upwards, sometimes to a vertical cylinder open at the top. The leaves are 1 - 2 mm. wide, subulate, deeply channelled and fairly rigid.

In the shoots, there are from 2 to 8 leaves, borne in two opposite ranks, with the basal sheaths enfolding around each other. Each autumn one or two of the most forward of the summer's shoots, lateral to the central shoot which has produced the inflorescence, become differentiated. These are designated front shoots, and usually have eight large leaves, (Figs. 2.1 and 2.2) enclosing buds and tiny leaves in their centre at the base. These terminate a lateral development (forward and downward) of the rhizome.

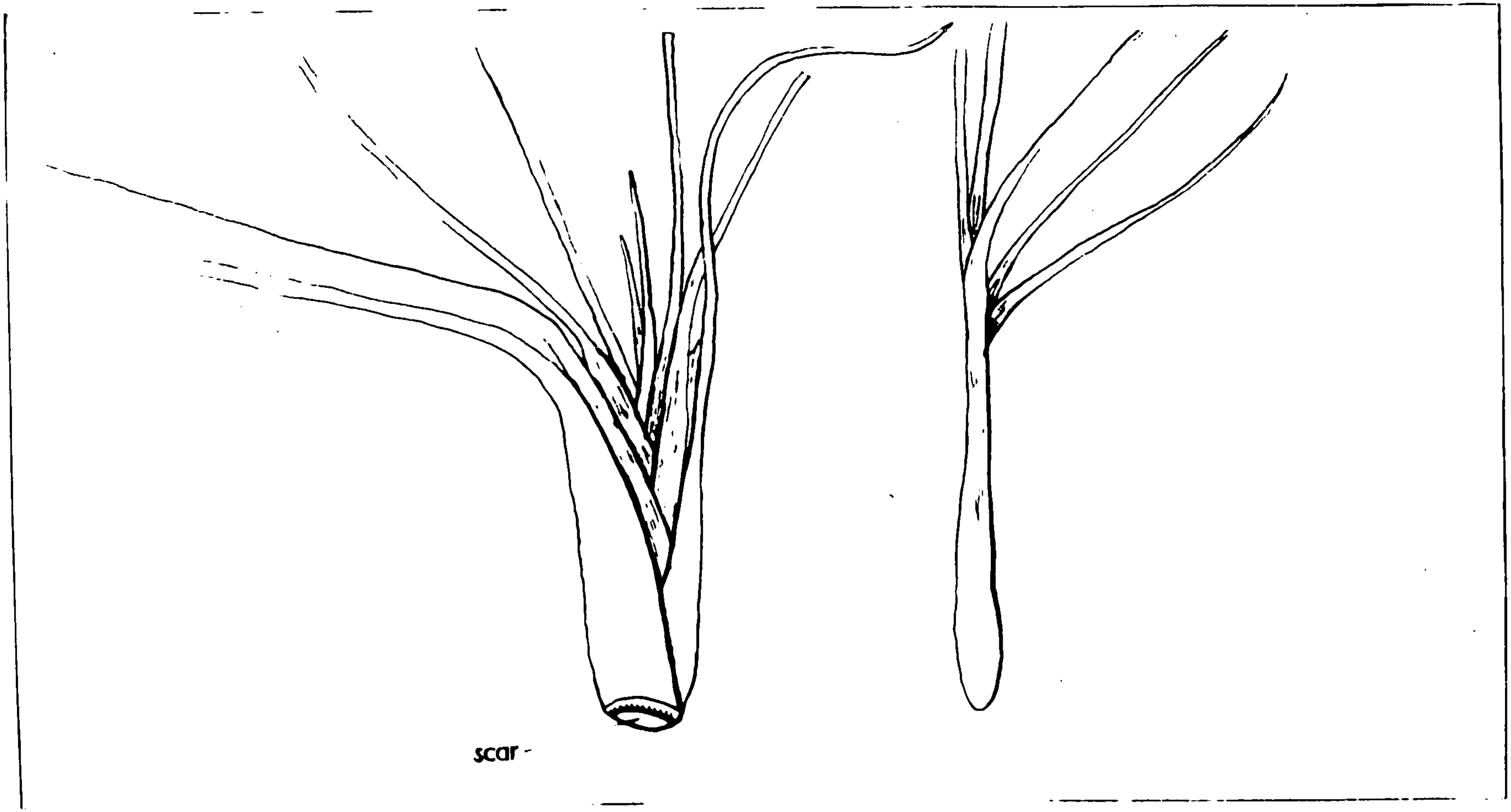


Fig. 22. Two views of a shoot at right angles to each other, showing the opposite leaf arrangement.

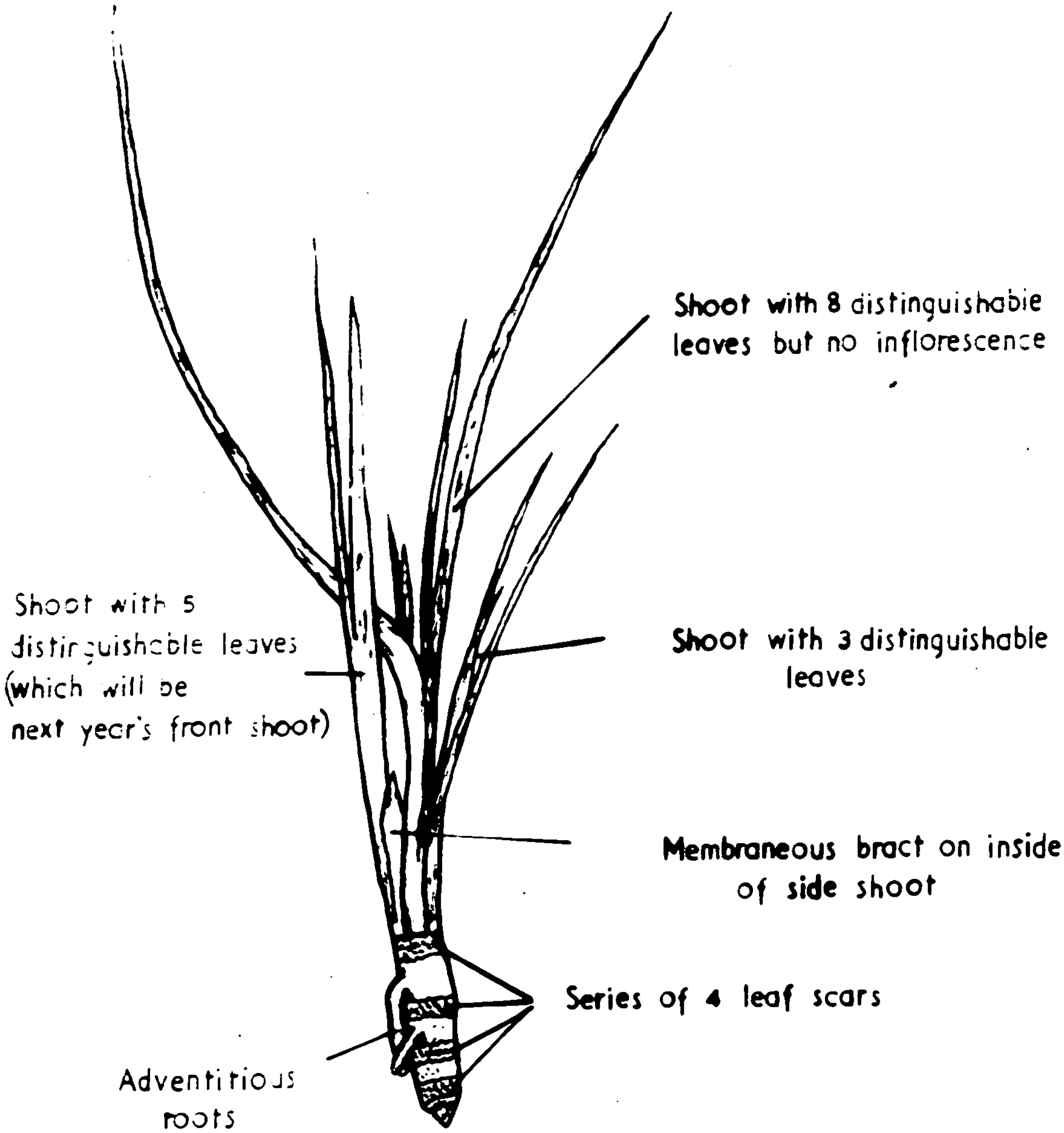


Fig 2·3 Young growth inside a front shoot, shown by removing the eight leaves of last year.

The buds and tiny leaves grow out rapidly next spring, and up to eight lateral shoots can develop from one front shoot. Individual leaves grow for about two months, only extending a little after this, but throughout the summer more and more leaves grow out from inside the sheathing shoot bases. The inflorescences appear from May to July, depending on the altitude and exposure, and the culms rapidly elongate to the height of 15 - 45 cm. Each front shoot usually gives rise to one inflorescence, but no inflorescence develops if the shoot is weak or in unfavourable conditions.

At first, only three shoots are apparent inside the front shoot (Fig. 2.3). The laterals are borne in the axils of the youngest (inside) leaves of the previous season, and contain two or four leaves. On their inside, separating them from the central shoot, are two short membranous bracts. The central shoot is subtended by two leaves, and contains about eight small leaves, but there is no sign of the inflorescence at this stage.

As it grows, the central shoot expands, forcing one of the lateral shoots forward out of the restriction of the two ranks of last year's leaves (Fig. 2.4). The central shoot also tends to move or grow forward, leaving the two ranks of four leaves at the back of the season's growth (Fig. 2.1). It is in this way that the plant moves forward through the soil and competing species.

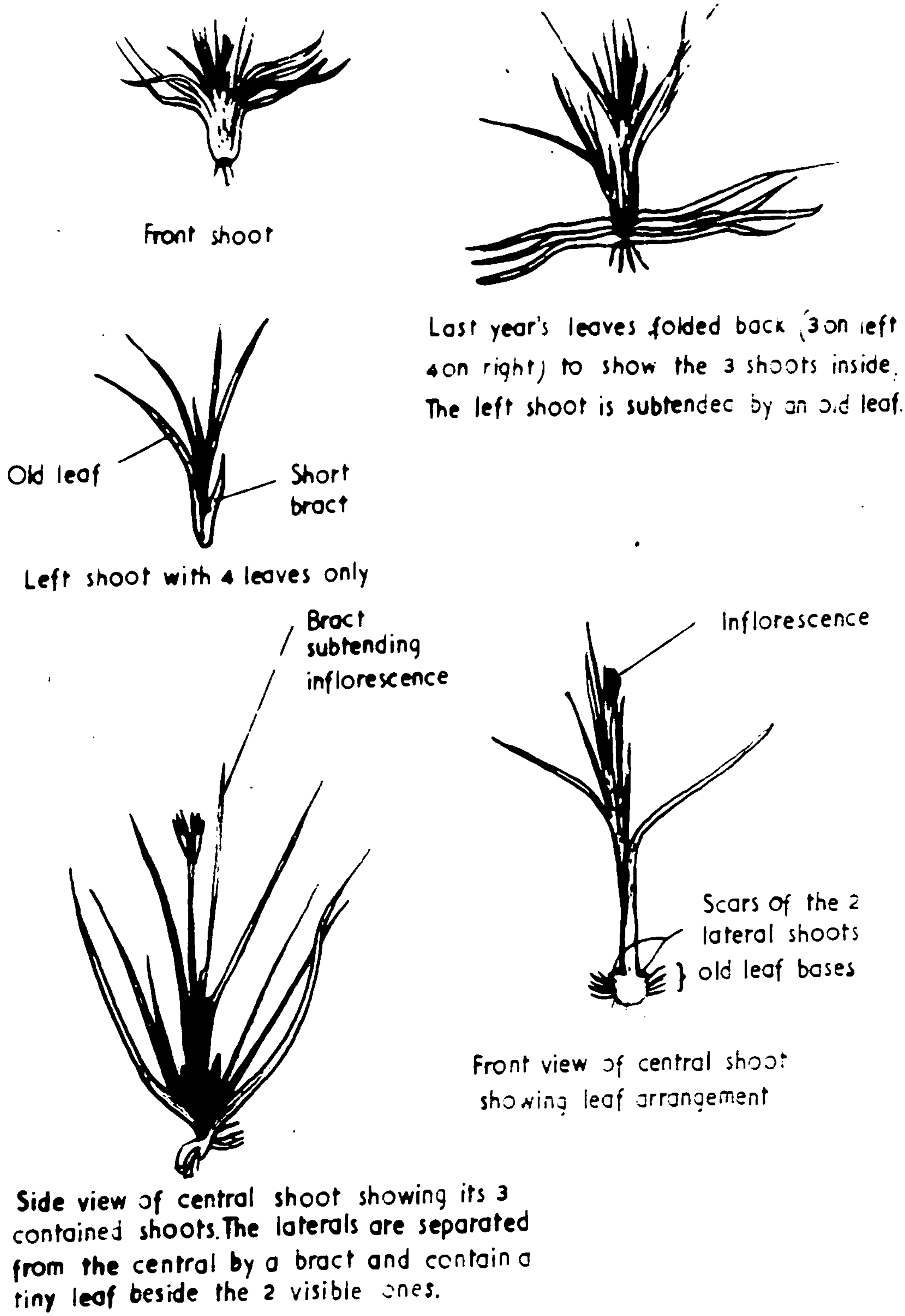


Fig 2·4. Dissection in July of last autumn's front shoot.

The break-out from last season's leaves allows adventitious roots to grow out from the young shoot bases. They extend rapidly down into the soil (the young roots averaged 10 cm. in length in mid-June, 1963 when the inflorescences began to appear at Moor House, and some had reached 15 cm. All had abundant root hairs). It may be that the formation of the inflorescence and next year's front shoots depends on the supply of nutrients which these young roots feed into the plant from ground which it has previously not exploited. Perhaps this is the explanation of the late start of inflorescence growth. Certainly it is the strength of the old leaves which causes growth to be restricted to a relatively narrow arc forward.

There next occurs a separation of two more lateral shoots within the central shoot, subtended by its two outer leaves. These two leaves are arranged at right angles to the two basal leaves which subtended the first lateral shoots, giving the appearance of decussate growth (Fig. 2.5), but it is probably a modified spiral arrangement. Again a short clear bract separates the lateral from the central shoot. At this time the inflorescence rapidly grows up and two or four further shoots may be produced inside the central shoot. The final culm is ensheathed by two leaves, one for only a short distance above its base.

Thus by rapid growth a single front shoot produces in one season a single inflorescence and a group of shoots around it, one or more of which will have become front shoots by next

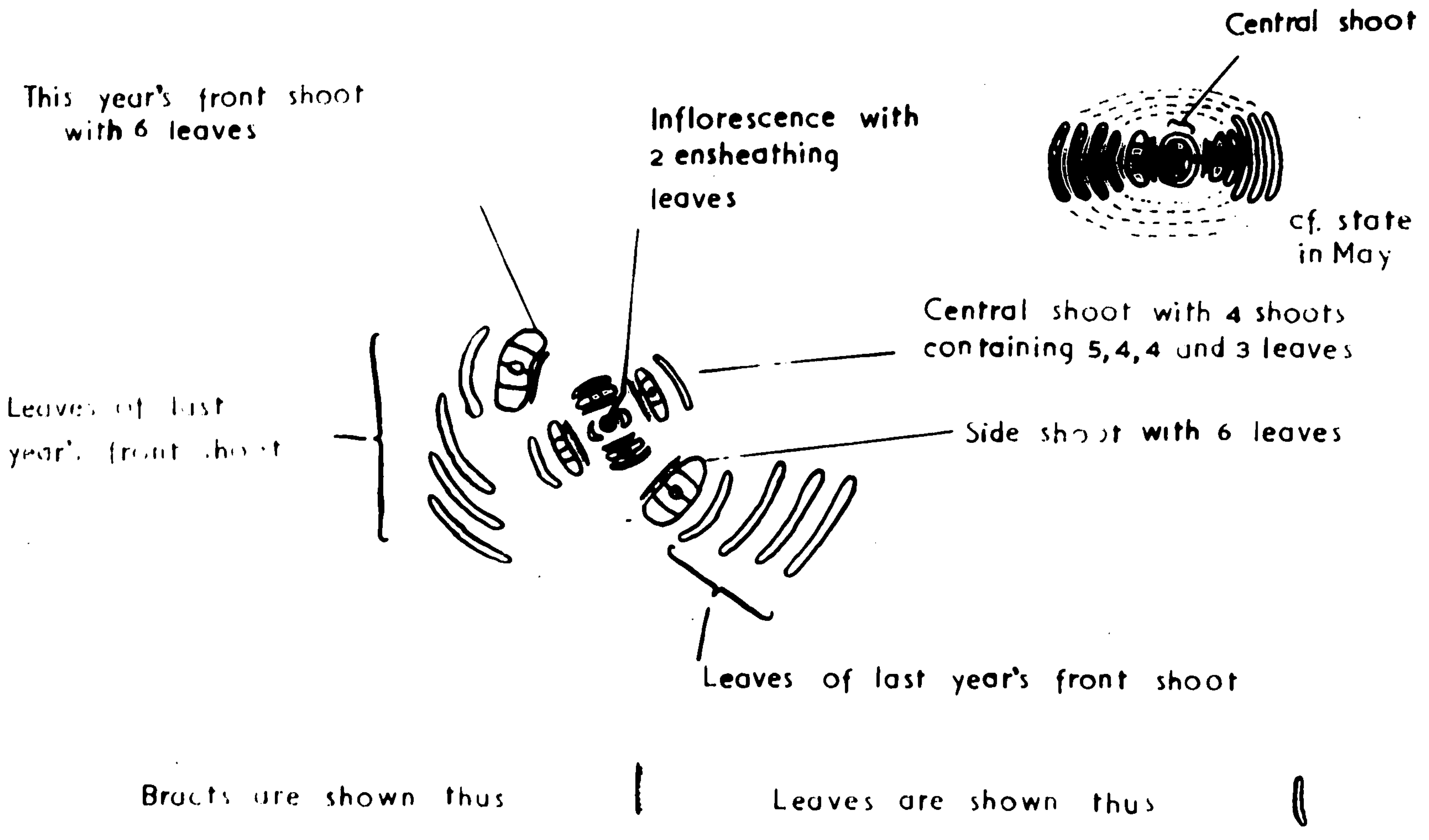


Fig. [illegible] Diagram of the front shoot structure in July after torsion.

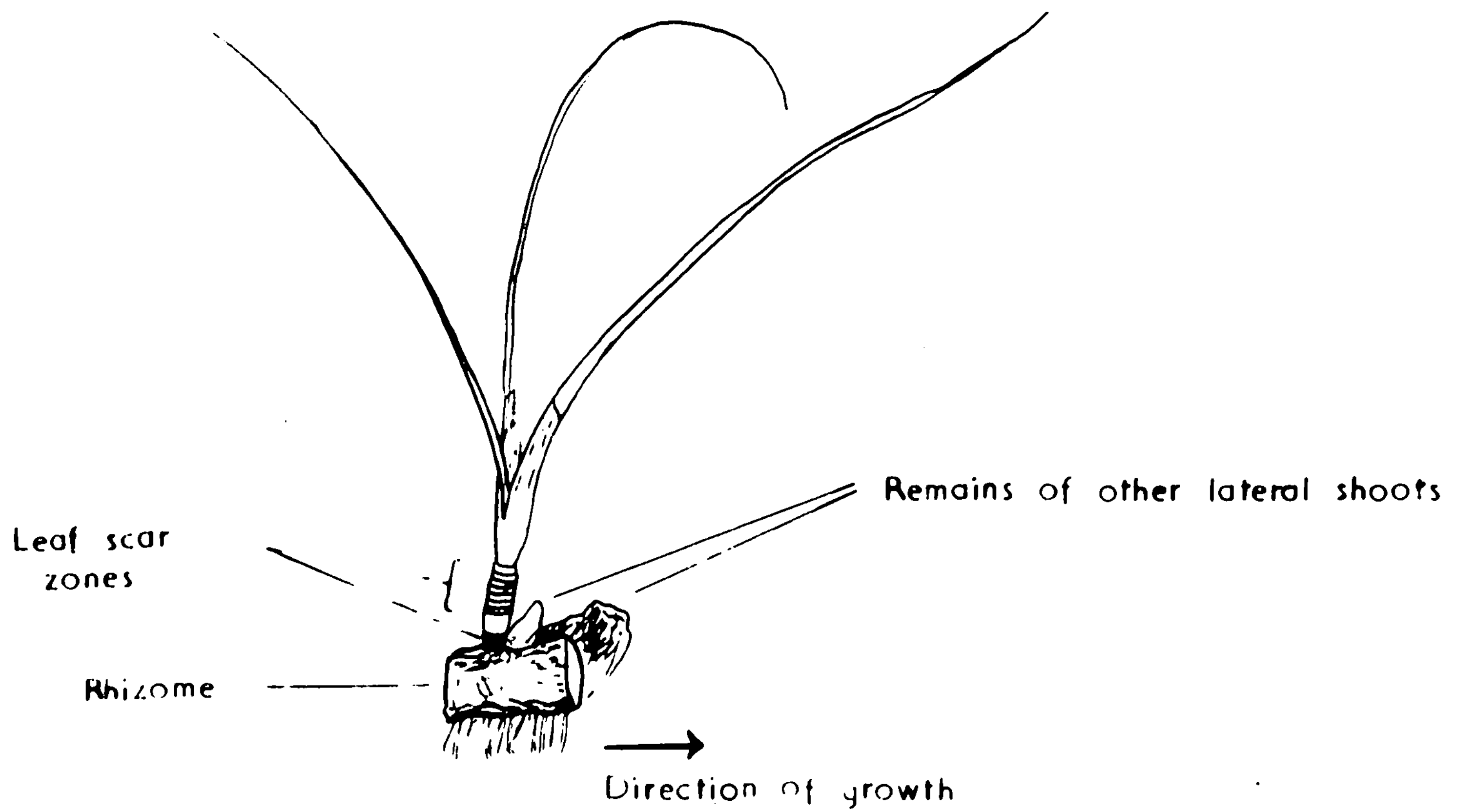


Fig 2·6. The rhizome stripped in the three year old section, to show a small shoot which has lived for 3 years. Two zones of leaf scars can be seen at its base.

autumn, ready to repeat the process next season.

Further growth also occurs in one-year old shoots, young leaves growing out from the centre. Last year's leaves are still photosynthetic during the next summer, being a darker green, but they turn brown in their second autumn. Occasionally leaves may be produced inside a shoot in its third summer (Fig. 2.6), but only rarely do these lateral shoots, left behind by the forward growth of the front shoots, give rise to inflorescences or branch to form new shoots.

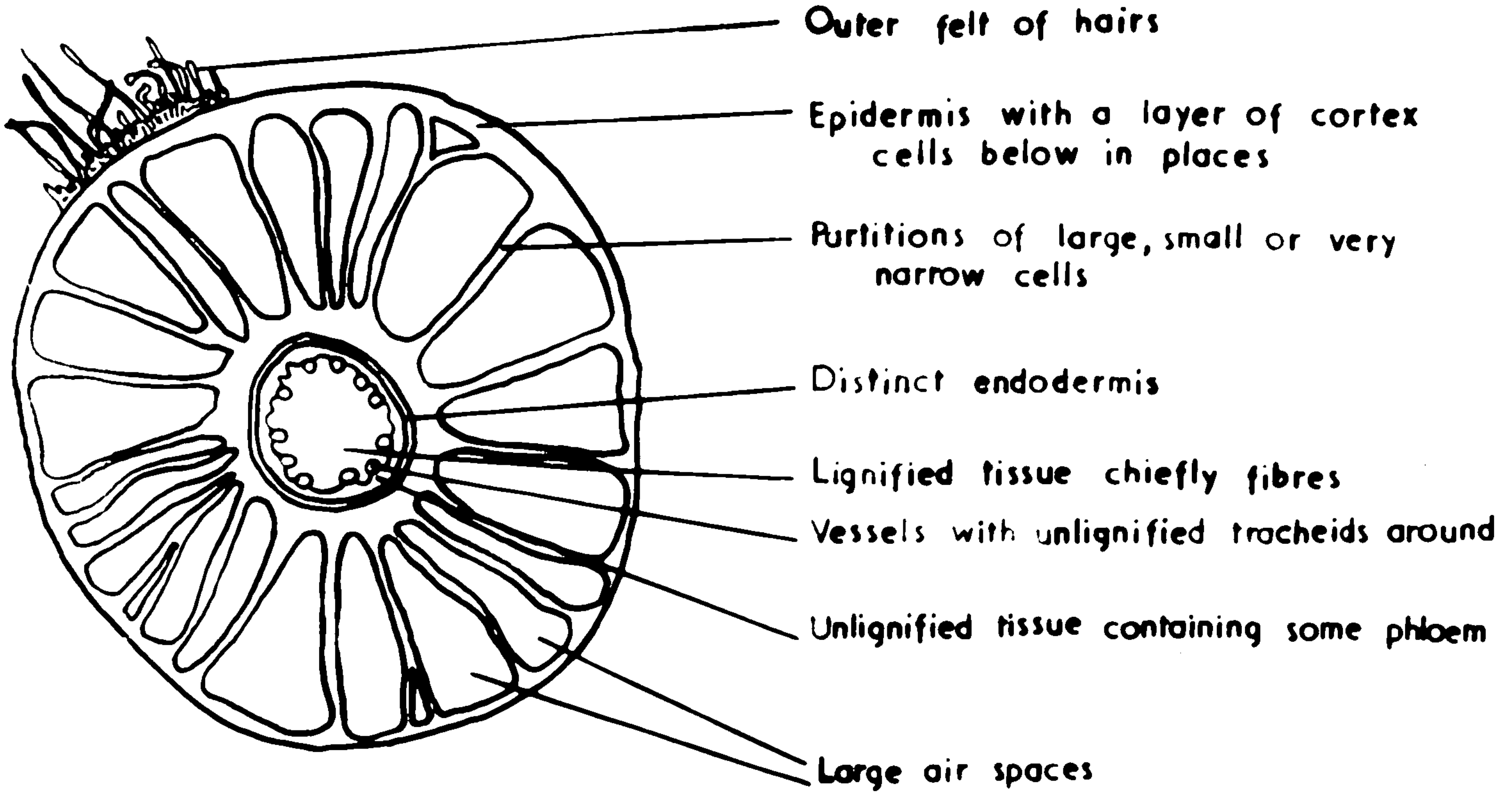


Fig 2·7 Tissue map of a T·S of a mature root.

B) Anatomy

A knowledge of the anatomy of a plant throws light on its competitive ability and habitat requirements. Whilst much has been written on the anatomy of Juncus squarrosus, especially by mid-Europeans, this is not readily available. Therefore a short descriptive account, together with a few diagrams, are here presented, in order to show several features which are important in determining the ecology of Juncus squarrosus.

The account has been divided to parts dealing with the root, rhizome and inflorescence stem, and the leaf.

The Root

A sizeable description is given by Freidenfelt (1904), together with an introductory section on the anatomy of the Juncus genus. Around a strong central stele, there is a system of large air spaces - see Fig. 2.7. They form part of an aerating system coming down from the leaves, the 'durchluftung'. The ratio of root to vascular cylinder diameter is 3.5, as opposed to 4.4 in J. effusus, 5.3 in J. biglumis and triglumis (Freidenfelt). Thus Juncus squarrosus has a greater amount of tissue devoted to water conduction, and less to aeration, than in these species, and correlated with this is its greater ability to withstand drought.

The root hairs are well-developed, forming a felt over the root surface. Their walls become brown and thick, and

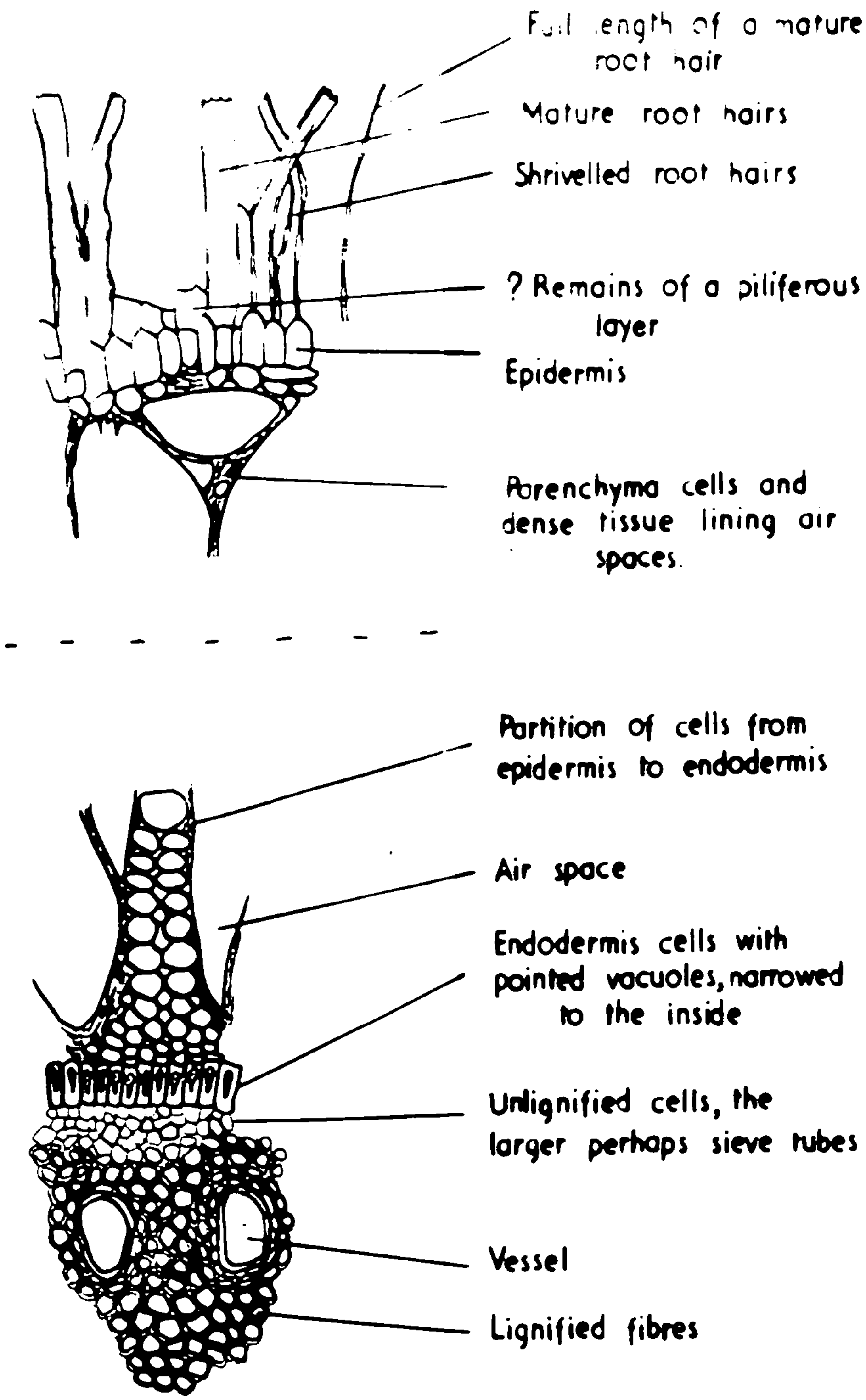


Fig 2·8. High-power T·S of a mature root.

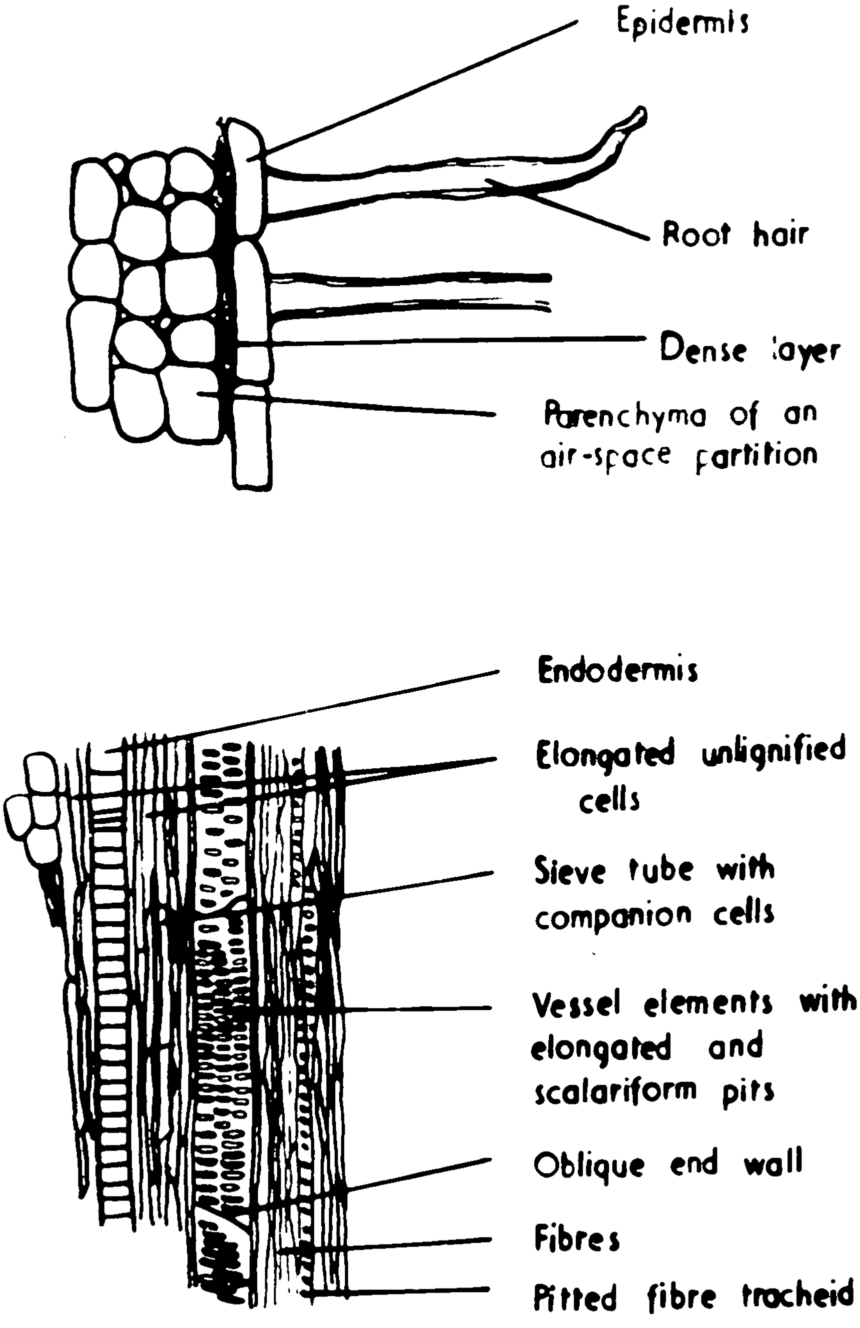


Fig 2·9. High-power L·S of a mature root.

Raunkiaer (1895) says the hairs have a long life, giving the plant a firm hold in the soil. The exodermis cells also have thick walls. In roots of the higher orders, the epidermis has larger, thin-walled cells, but it is soon discarded. The hairs in these roots are absorbing, having fairly thin walls.

The cortex contains about ten rows of cells. They collapse during the formation of the air spaces, and become pressed together into inner and outer layers. This occurs some distance back from the root-tips, during the first season. Radial partitions are left, dividing up the air spaces.

An endodermis of tall, very thick-walled cells (Fig. 2.8 and 2.9) surrounds the central cylinder. This contains about 10 large vessels around a pith of very thick-walled fibres. Outside is a thin zone of unlignified cells, containing the phloem. In the finer roots there are fewer vessels, the cortex consists of fewer layers of cells, but the endodermis is still present.

The Rhizome and flowering Stem

The general structure of the rhizome is shown in Fig. 2.10, whilst Fig. 2.11 gives drawings of some of the cells. The epidermis and suberised cell layers below are much broken. In the cortex parenchyma are air canals, much smaller than the air spaces in the root, and numerous vascular bundles, which run to the adventitious roots. There is a distinct endodermis

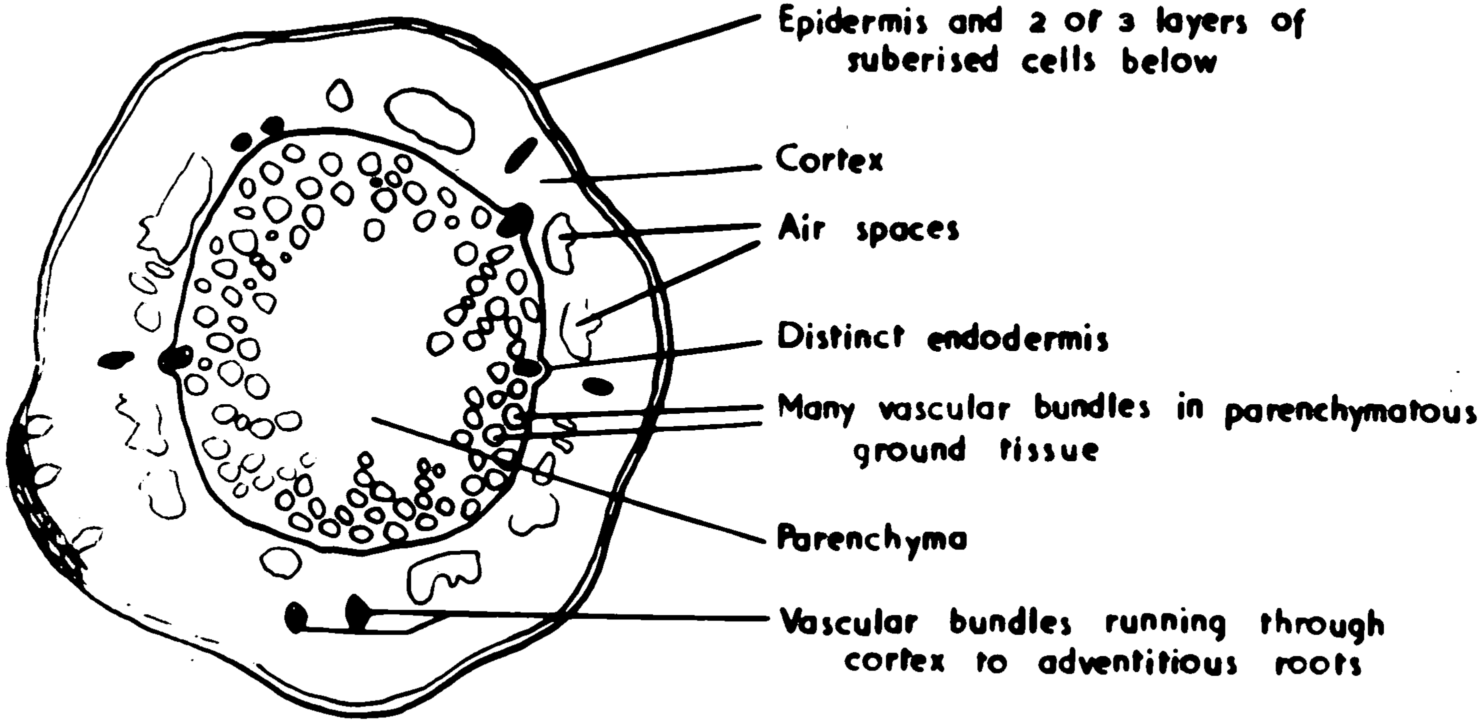


Fig 2·10. Tissue map of a T·S of 2 year-old rhizome (approx. 20x).

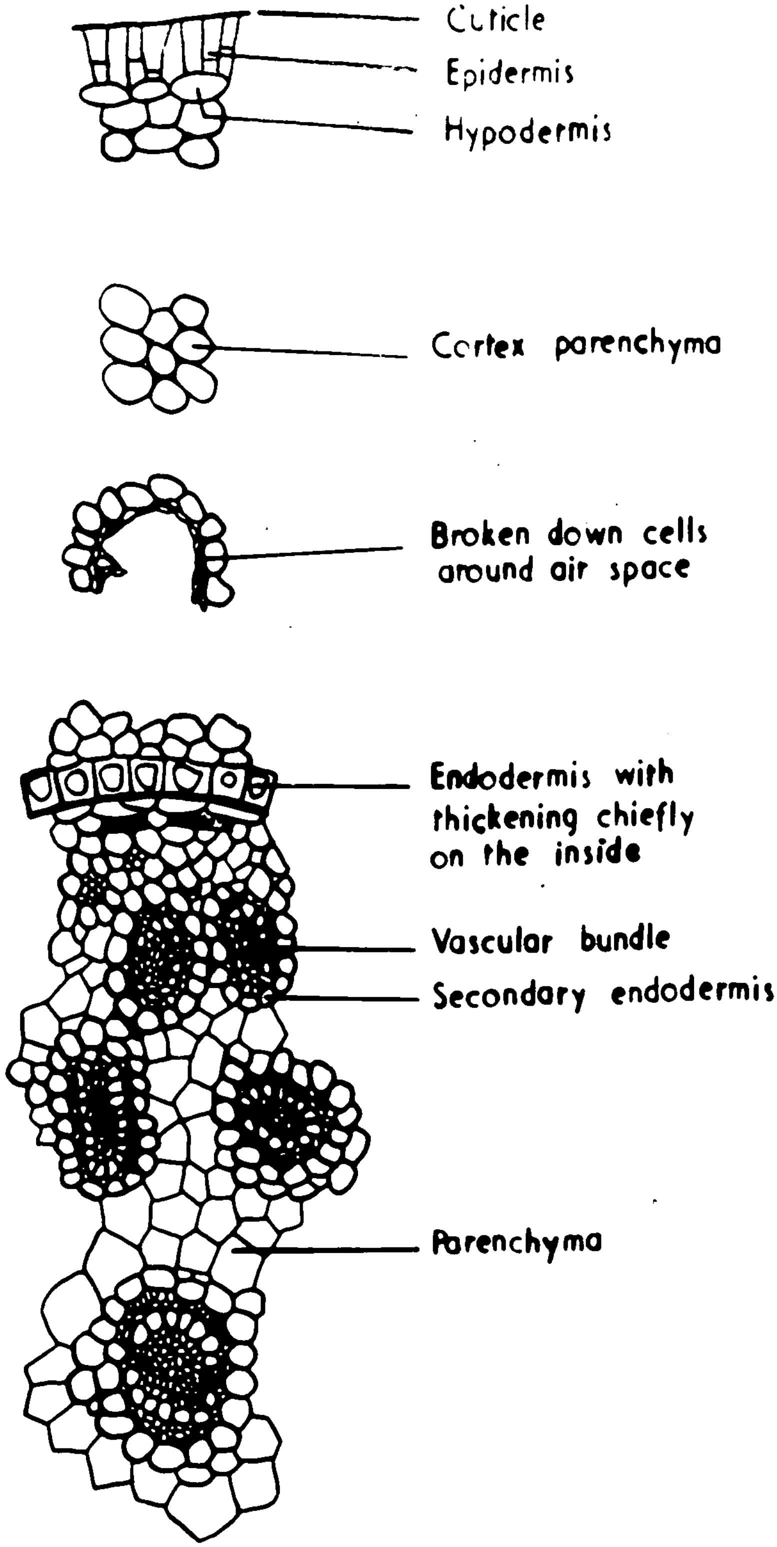


Fig 2·11. High-power T·S of 2 year-old rhizome.

around a large central area containing many vascular bundles in a parenchymatous ground tissue.

In the flowering stem, as described by Blau (1904), the epidermis walls are strongly thickened, especially on the outside. Some stomata are present. Below are three to four rows of palisade cells. The aerating cells are only weakly developed amongst the cortex parenchyma. The central cylinder is formed by a thick ring of sclerenchyma, containing the vascular bundles, inside which is a large pith.

The Leaf

A considerable amount has been written about the evolution of the leaf in the Juncaceae, and several workers including Adamson (1925) and Peisl (1957) have discussed the structure of the leaf of Juncus squarrosus as part of the series leading to the circular type of leaf as found in J. effusus. Blau (1904) also gives a full description.

Near its base the leaf has a bifacial structure with a broad channel in the adaxial surface. Passing upwards, the leaf becomes narrower and thicker, and close to the tip the adaxial surface, which has no bundles below, forms only a quarter of the apparent upper surface (Adamson).

The upper epidermis has large swollen cells which are thick-walled, as are the cells of the lower epidermis. In the middle of the leaf channel there are only three or four rows

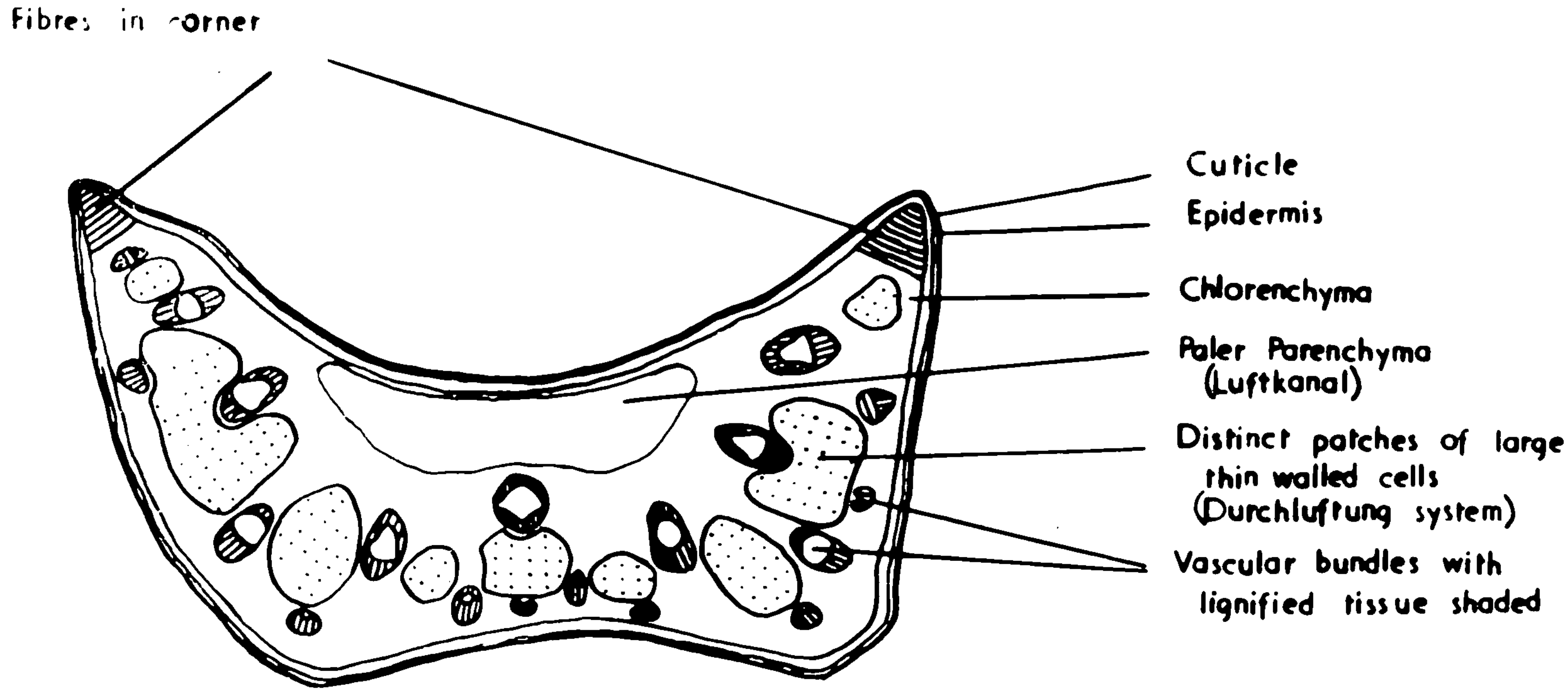


Fig 2·12 Tissue map of a T·S of a one-year old leaf (approx. 40x).

of thin-walled hypodermal cells separating a large flattened air canal from the epidermis (Fig. 2.12), but chlorenchyma is below the epidermis throughout the rest of the leaf. Stomata at 300 per mm^2 are more numerous than in many Juncus spp. according to Blau.

There are two rows of vascular bundles, arranged in a broad U, which becomes more closed towards the leaf tip. Between the bundles there are aerating canals, formed by large thin-walled parenchyma cells. The vascular bundles (Fig. 2.13) are surrounded by a distinct endodermis, and have large caps of fibres at both ends. Inside the xylem and phloem have the usual monocotyledon arrangement.

At each corner of the leaf there is a further group of fibres. The overall effect is to make the leaf very strong, and thus xerophytic, being resistant to wilting, and very tough, and thus not palatable to grazing animals.

Conclusions

Juncus squarrosus can grow in a wide variety of habitats, ranging from dry to completely waterlogged, as its structure incorporates the necessary adaptations for growth under these different conditions. The abundance of sclerenchyma and the thick walls of the epidermis cells make the aerial parts resistant to drought, whilst the aerating system makes the roots independent of ground water for gaseous exchange.

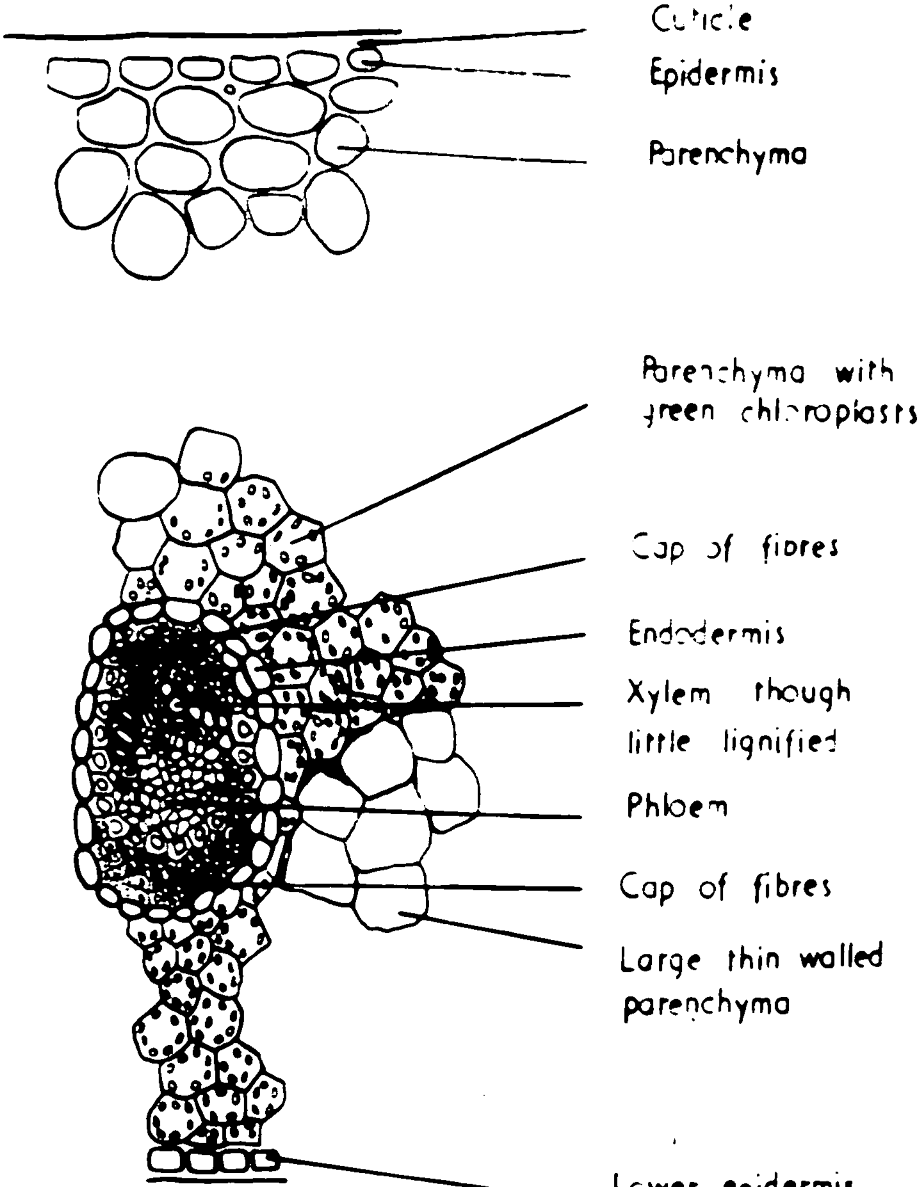


Fig 2·13. High power T·S of a one-year old leaf.

However, as will be discussed later in the thesis, *Juncus squarrosus* does not grow fast and can withstand little competition.

SECTION III. REPRODUCTIVE CAPACITY.

The topics dealt with in this section are the production of seeds, their dispersal and the number that germinate. A knowledge of these values, and how they are affected by habitat and climate, is very necessary to the understanding of how the species maintains itself and spreads to new localities. The seed production and germination %s were found for a variety of community types, many of the sites being used in the phytosociological analysis described in section 6.

A) SEED PRODUCTION

The seed production of a plant is controlled by four of its attributes:-

1) The number of inflorescences produced.
2) The number of florets on the inflorescences.
3) The number of florets that ripen to fruits (capsules).
4) The number of seeds in the capsules.

Since *Juncus squarrosus* is usually one of the more prominent plants in a sward, the total area it occupies in a place can be found more easily than the number of plants, and it was therefore thought useful to relate seed production to area. Furthermore, this avoids difficulties due to the uncertainty of deciding what is a shoot or plant of *Juncus squarrosus*.

Each attribute was measured, to single out the ways in which the different factors limit seed production. Also it was hoped that entomologists, working on the moth *Coleophora alticolella* Zell., would find the data useful, and some of their previous data are incorporated into the present results. The larvae of this moth infect the capsules of *Juncus squarrosus*, eating the ripening seed.

Methods

The 1/4 sq. m. quadrats used in the phytosociological recording were left marked by stakes, so that the inflorescences could be collected when the capsules had ripened. This procedure was adopted to prevent bias in the results caused by selection of areas of *Juncus squarrosus* when the inflorescences were visible. Siting of the quadrats was necessary for the measurement of the inflorescence production per unit area. Otherwise the variable amounts of other communities included in the quadrat would cause large variation, and result in the inflorescence density being lower than in the *Juncus squarrosus* community. If more and larger quadrats were cast at random, the numbers of florets, capsules and seeds would be quite unmanageable.

Inflorescences were collected from 20 quadrats at each site, a harvest being taken from a second quadrat alongside each of the 10 marked quadrats used in the phytosociological recording. A brief description of the sites is given in Appendix 1, and their locations are shown on Fig. 1.1.

The first harvests were taken at the lowest site (Dipper F) on 11th August, 1962, and 23rd August, 1963. The timing was determined by the need to avoid losing any seeds due to dispersal before harvest by splitting of the capsules, and the need to allow development to continue as long as possible. This is a source of error in the results at the lower altitudes, for seed development would normally be going on after the more mature capsules had split, and the seeds had been dispersed. In 1962 florets were still showing anthers at the Moor House level (1850 ft.) in early September, and very few capsules had formed. Better weather at the end of the month and in early October speeded ripening, and all the other sites were harvested between October 9th and 17th. In 1963 ripening proceeded more rapidly and most sites were harvested by September 13th; the final two on the fell tops on October 2nd.

Besides these harvests in predetermined areas of a fixed size, certain others were taken in both years, and in 1961 also, to compare attributes controlling seed production at different places away from the Moor House area. A further purpose was to obtain information on Coleophora infestation. In 1961 an initial transect was made up ~~from~~ the Tees Valley from the junction with Trout Beck to the summit of Cross Fell. Whilst these harvests were not related to area - at some sites quite a stretch of ground had to be covered to gather the inflorescences - great care was taken after experience with the initial transect, to collect every inflorescence at hand, large or small, without selection.

Once indoors, the number of florets and capsules on each inflorescnece was found and noted, and the average calculated for each quadrat, whilst the number of inflorescences from each quadrat was found, and the average found for the site. Inflorescences grazed by sheep were included in the figures for Infl./Q., but excluded from the inflorescence number used in the calculation of thefloret and capsule ratios, as they did not contribute to the floret and capsule totals.

The two further samples given in Appendix 4 for site F (Dipper) satisfactorily confirm that the number of florets per inflorescence and the number of capsules did not increase after the initial August harvest, for which data are given in Appendix 1.

Inflorescences with capsules were kept in glass tubes or polythene bags in a dry place, so that capsule maturation could continue, and after 4 to 5 weeks the seeds were extracted using forceps. To keep down germination trials to a minimum, but maintaining replication, capsules from adjacent quadrats at a site were pooled, so that ten measures of seed production were obtained from each site.

On extraction the seeds were counted, and some packeted in fifties, ready for the germination trials. In addition, seeds from 20 capsules from each site were counted singly after careful slow dissection, to check if the number of seeds per capsule varied from place to place. These results are given in Table 3.8, but the seed/capsule figures given in the Appendices are the ratios of the total number of seeds extracted to the total number of capsules at each site.

At this stage it is necessary to say what were counted as florets, capsules and seeds. Florets gave no trouble except when they had failed to separate in some underdeveloped inflorescences at high altitudes. Here as many as possible of the florets were counted by eye, but in some cases there were tightly adpressed glumes at the base of the inflorescence, which represented an unknown number of undeveloped florets. These were ignored.

The florets in which the ovary had expanded, forcing the glumes apart, were counted as capsules. All these contained developing seed, but when seed extraction was done, some had such tiny seeds that they could not be distinguished from replum or wall debris, and these were ignored. It is very doubtful whether such seeds would ever be dispersed, and then whether they could germinate, as the weather deteriorated after both harvestings, and maturation would cease. Slightly larger seeds, certainly recognisable, were counted in the seed number, and kept together with full-sized seeds, two or three times as big, for the germination trials.

Results and Discussion

a) The effect of sheep grazing

The developing florets of *Juncus squarrosus* are nibbled off the inflorescence stalk by sheep. On harvesting, such inflorescences are plainly noticeable, having either a broken stalk, or only the base of the glumes remaining at the top. These inflorescences were counted and shown in Appendices 1 to 4 as a % of the total number of inflorescences.

At some sites sheep considerably reduce the reproductive capacity. On Cross Fell, for example, 57.9% of the inflorescences were eaten in 1962, and on Pendle Hill at 1350 ft. 72.2% were eaten in 1963. These places are usually well-drained and grassy, with *Festuca ovina* dominant and only patches of *Juncus squarrosus*. *Festuca* grasslands normally bear a much heavier grazing pressure than *Juncus squarrosus* areas or blanket bog, and it would seem that the sheep are grazing *Juncus* from convenience rather than preference. On the more typical *Juncus squarrosus* areas on peaty gleys or peaty podsols, it is rare that more than 10% of the inflorescences are eaten.

b) <u>The factors affecting the inflorescence number per quadrat</u>

It can be seen from the composite histograms of Fig. 3.1 that there is not a close correlation either between the number of inflorescences produced in two succeeding years, or between the inflorescence and rosette numbers in the 10 quadrats at each site. Each rosette counted consists of several shoots which may or may not produce inflorescences in a season. Changes in the vigour of rosettes may thus lead to considerable variation in the inflorescence number in a quadrat.

As the quadrats were deliberately sited to include only <u>Juncus squarrosus</u> areas, most contain over 10 rosettes obscuring the relationship. Only at site I, initial colonisation after peat erosion, where <u>Juncus squarrosus</u> is the only important species, is the inflorescence number related closely to rosette number. At this site too there is a better relation of rosette number and cover than at the others (see Fig. 5.3).

But neglecting individual quadrats, a general relationship can be seen between total rosette number and total inflorescence number, sites with few rosettes per quadrat having fewer inflorescences, e.g. F - Dipper, D - Leat and E - House limestone grassland. The average is about 1 inflorescence per rosette, but several sites differ. Trout Beck Foot - B and House Hill colonisation - I have a greater

Table 3.1. Comparison of 1962 and 1963 Reproductive Capacity, with 95% confidence limits.

Site	Infl./Quadrat 1962	Infl./Quadrat 1963	Florets/Infl. 1962	Florets/Infl. 1963	% florets ripened to capsules 1962	% florets ripened to capsules 1963
G Cross Fell	16.1± 6.23	5.0± 0.75	6.28± 0.53	7.2± 2.75	0	0.02
A Knock Fell	24.7± 6.04	16.7± 4.83	7.84± 0.30	7.4± 0.33	0	1.6
L Rough Sike Head	32.6± 8.41	9.8± 2.56	7.64± 0.29	5.9± 0.42	0.43	19.0
J House Hill recolon.	21.5± 1.59	19.6± 5.62	10.31± 0.44	10.4± 0.43	5.2	48.8
I House Hill initial	48.1±17.42	27.4±14.90	7.71± 0.36	10.1± 0.57	1.8	54.2
C Moss Burn alluvial	14.4± 4.23	17.2± 1.93	14.13± 0.76	10.9±00.68	9.5	60.3
E House limestone grassland	6.45± 2.95	8.0± 3.64	9.63± 0.77	9.6± 0.59	2.5	49.5
K Pasture peat	22.0± 5.23	18.4± 5.27	11.61± 1.44	9.7± 0.38	4.3	62.1
H Teesside green slopes	14.4± 5.26	21.6± 6.15	9.54± 1.62	11.9± 0.41	5.7	51.0
D Lite bank	8.7± 1.10	12.2± 3.56	11.74± 0.93	13.4± 0.76	12.4	58.7
B Trout Beck foot	32.4± 2.11	41.4± 5.25	6.39± 1.06	8.2± 0.54	3.9	48.9
F Dipper	11.6± 4.83	14.7± 3.42	13.52± 0.70	14.2± 0.68	52.3	61.4
Average of 12 sites	21.1	17.7	9.7	9.9		

Plate 3 - Section 3: The initial colonisation of the spread of peat and sandstone debris left after peat erosion.

number of inflorescences, the inflorescence ratios being 1.6 and 2.3, whereas the ratios are 0.4 at Cross Fell - G, 0.7 on the Leat - D and 0.6 on the House limestone grassland - E. This is perhaps a reflection of the vigour of the plants, those at site I being young and not experiencing competition from other species (see Plate 3). In contrast, conditions are severe on Cross Fell, with a short growing season and a difficult substratum of a well-drained stony shallow soil. Sites D and E are also rather marginal for Juncus squarrosus, being fairly well-drained.

As seen in Table 3.1 and Fig. 3.1, there is little difference in the number of inflorescences produced in the two seasons 1962 and 1963. But the three high-level sites have significantly fewer inflorescences in 1963, and this may have been caused by the previous weather conditions (cold snowy winter in 1963, following a poor summer in 1962) which had a greater effect on the vigour of the plants here than at lower altitudes.

Reay (1958) recorded a very low number of inflorescences in 1957 (Table 3.2), and it would seem that this is associated with drought conditions in spring (Table 3.3). Unfortunately I was not able to make parallel observations.

Table 3.2. The effect of season and altitude on the number of inflorescences per sq. m., with 95% confidence limits (after Reay).

Altitude (feet)	Year 1955	1956	1957
1500	104.0±10.4	167.6±18.4	7.3±4.2
1550	88.0±11.4	118.7±16.6	1.3±1.1
1600	115.2±13.6	156.9±20.2	3.5±2.2
1650	105.6±16.0	122.4±16.2	4.3±3.0
1700	91.2±11.8	117.4±22.0	1.8±2.1
1750	91.2±13.4	105.9±22.2	6.5±3.0
1800	108.8±16.0	98.4±25.2	11.3±5.8
1850	88.0±16.0	32.6±14.4	1.0±1.2

Table 3.3. Spring rainfall (inches) during the last 11 years at Moor House.

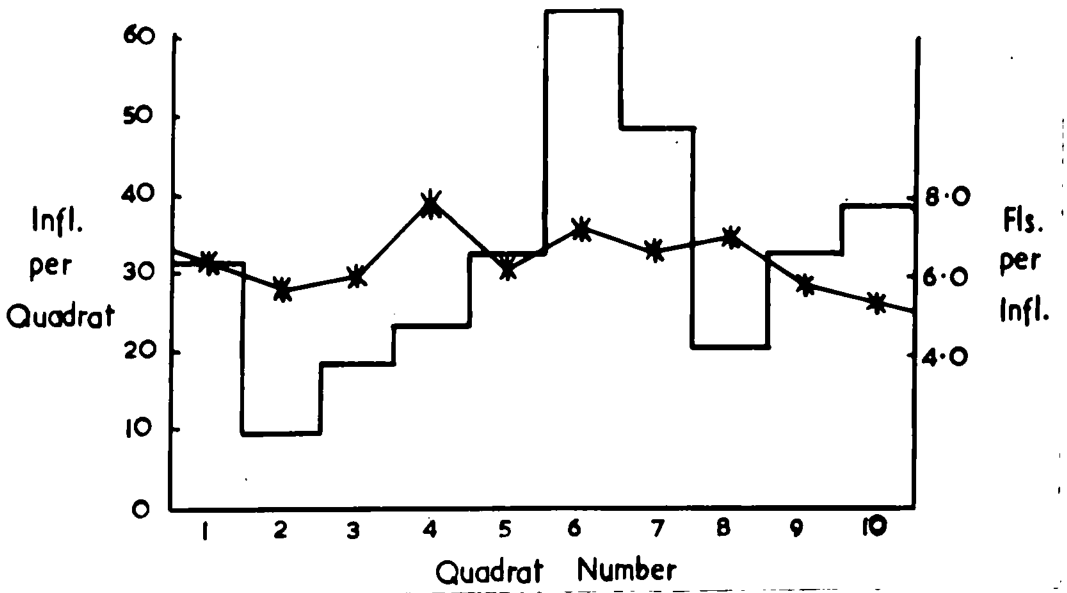
Year	April	May	June	Total
1953	7.44	3.52	4.03	14.99
1954	1.76	6.80	7.40	15.86
1955	3.94	8.89	4.26	17.09
1956	2.19	3.91	3.77	9.87
1957	1.51	3.86	2.13	7.50
1958	2.76	6.39	4.39	13.54
1959	8.46	1.35	4.05	13.86
1960	4.96	2.51	3.02	10.49
1961	4.60	3.55	3.30	11.45
1962	7.34	5.37	3.11	15.82
1963	6.22	6.39	6.41	19.02

c) <u>the factors affecting the number of florets per inflorescence</u>

1. Inflorescence number

The fls./infl. ratio is fairly constant at a site, shown by the low confidence limits attached to its values in Table 3.1 and the Appendices. Examination of the individual quadrat data shows that the production of a large number of inflorescences in a quadrat does not affect the fls./infl. ratio (see Fig. 3.2). But sites with a high infl./Q. ratio have a low fls./infl. ratio at that particular altitude, e.g. B with 6.4 fls./infl. and 32.4 infl./Q. and I with 7.7 fls./infl. and 48.1 infl./Q in 1962. The explanation suggested is that unfavourable conditions limit the floret number (B - lack of shelter and well-drained, I - poor soil conditions), but the lack of competition allows the plants to be vigorous and some produce many inflorescences.

Fig. 3.2. The relation of inflorescence number and floret per inflorescence ratio in 10 quadrats at site B in 1962.



2. Climate

Changes in either the micro-climatic or soil conditions can cause a very marked difference between the fls./infl. ratio of two sites, though the other factor remains constant, or even appears to be acting in the reverse direction. Thus the transect up the S.E. escarpment of Pendle Hill (Appendix 3) has a small drop in fls./infl. ratio from 1150 to 1550 ft. on one soil, but it is higher at 1750 ft. on a different soil type.

The surprising difference between the Trout Beck Foot - B and Moss Burn - C alluvial sites is correlated in large part with microclimate. They have Juncus squarrosus communities very similar phytosociologically on similar soil types, but the Moss Burn quadrats are well-sheltered in the narrow stream bottom, whereas the Trout Beck Foot quadrats are in a wide plain at the Trout Beck - Tees junction.

Exposure is such an important part of the affect of climate that it is not easy to avoid it in assessing the other affects, whose incidence varies with altitude. It is very difficult to find two sites with similar exposure and a similar soil over 200 ft. apart. But there does seem to be a gradual reduction of floret number with altitude. Thus sites L and K are of quite similar exposure and soil type, and the fls./infl. ratio falls from 11.6 at 1850 ft. in the Moor House pasture to 7.6 at2300 ft. at Rough Sike Head. The high values down the

Table 3.4. Maximum floret and capsule numbers on an inflorescence at the different sites in different seasons.

Year Site and altitude (feet)		1961 fls.	caps.	Site and altitude		1962 fls.	caps.	1963 fls.	caps.
Tyne Valley				Moor House series					
Lee House	1400	64 +	16	F (in Tyne V)	1550	57	32	37	33
Snead	1650	19 +	12	B	1750	23	6	27	14
Tees to Cross Fell transect	1750A	20 +	14	D	1775	26	12	32	24
	1750E	20 +	15	H	1800	34	9	27	22
	1975A	22 +	9	K	1850	32	5	21	21
	1975E	22 +	9	E	1850	25	3	25	16
	2250A	27 +	15	C	1850	39	11	32	21
	2250E	27 +	8	I	1900	23	4	28	19
	2500	20 +	1	J	1900	35	8	26	15
	2650	15 +	0	L	2300	20	2	14	5
	2725	20 +	1	A	2450	17	0	15	2
	2925	15 +	0	G (= 2925 on Cross Fell)		15	0	16	1

\+ small samples, such that there is a chance that the inflorescence with the highest number of florets or capsules at a site was not gathered.

Tyne Valley (Dipper (F), Lee House, etc.) do seem significantly higher than for the sites around Moor House, with the exception of Moss Burn (C), which is especially sheltered.

A similar picture is shown in Table 3.4. Inflorescences from the Tyne Valley with 57 and 64 florets are considerably greater than any from around the Moor House level. Of these, site C again comes the highest with 39 florets in 1962 and 32 in 1963. The difference between sites K and L is maintained - 32 and 20 in 1962, and 21 and 14 in 1963. Presumably the floret number is not determined by the weather during flowering, but by previous seasons.

3. Soil

Taking values for fls./infl. from the Appendices into account besides those in Table 3.1, it can be said that low fls./infl. ratios are found on well-drained, base-deficient soils (which also have smaller plants - Table 5.1) e.g. Cross Fell 6.3, Withnell 6.1, and the three escarpment sites on Pendle Hill. Small-sized plants in the herbarium of the British Museum from heathy places in the S. of England also had few florets. Thus an unfavourable soil will keep the floret number low no matter what the micro-climate is. But in unfavourable climates, as above 2500 ft. at Moor House, soil conditions still influence to a great extent the floret number e.g. 10.9 fls./infl. in 1961 on a peaty podsol at 2725 ft.,

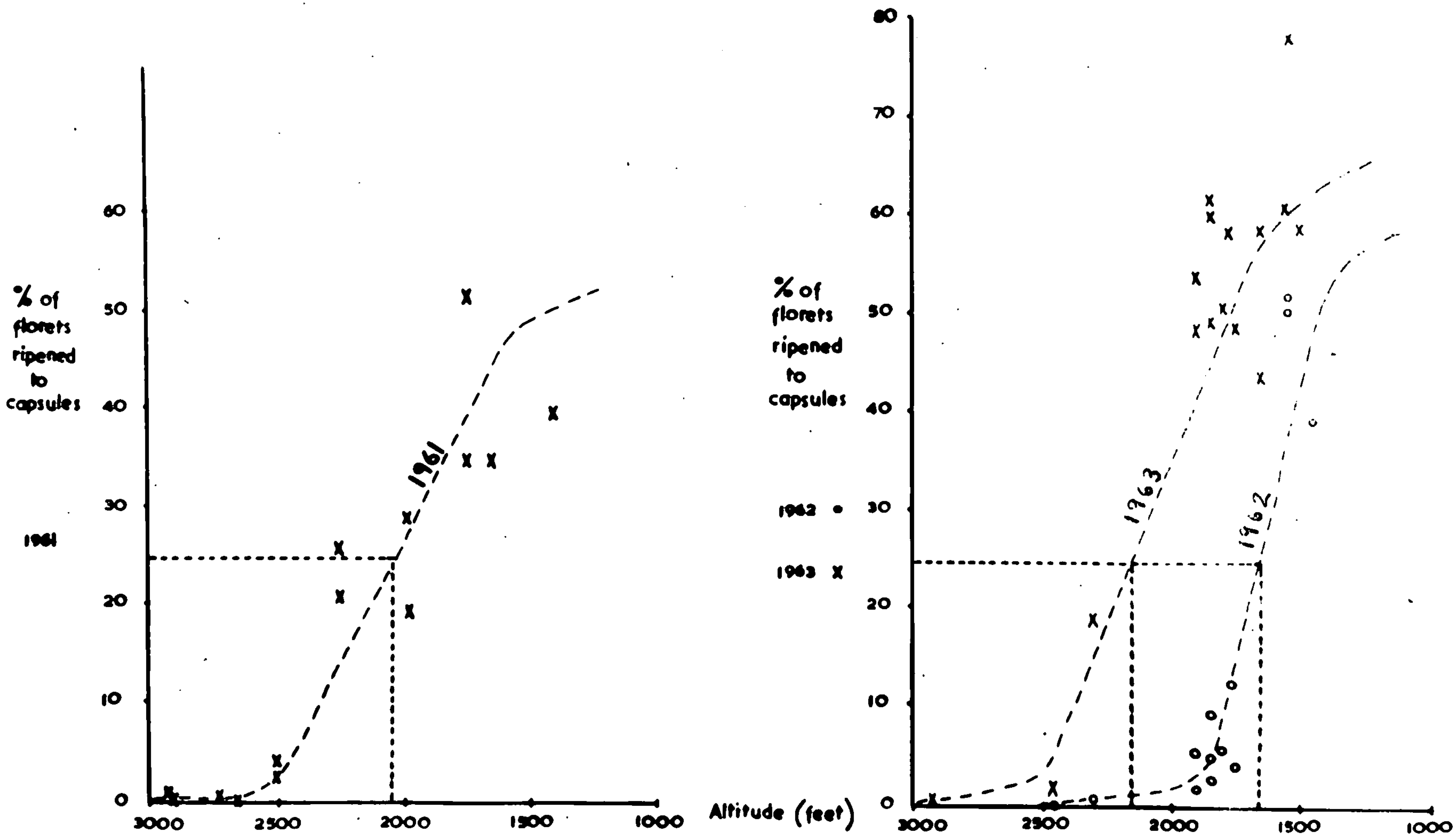


Fig. 3·3. The relation of capsule ripening to altitude and season in the Moor House area.

but 3.7 on the stony solifluxion soil, a mountain-top podsol, at 2925 ft. on Cross Fell. The average height of these inflorescences was 25 and 17 cm. respectively.

It thus appears that soil is the primary control on floret number per inflorescence, and climate is a secondary influence.

d) The control of capsule formation

The number of capsules formed per inflorescence is governed by the number of florets and the amount of maturation that occurs. The values for % florets ripened to capsules given in Table 3.1 and the appendices were obtained from the total number of capsules and florets at a site, and reflect the amount of maturation.

There is no indication that this is affected by anything other than the micro-climate. One might have expected plants on a warm, well-drained soil to have started development sooner, but the values for sites E and B, which approach nearest to this, are lower than for other sites at the same altitude. That the value for B, Trout Beck Foot, is low (3.9% in 1962) as compared with C, Moss Burn, (9.5%) is a further indication of its lack of shelter.

A comparison of the values in 1961, 1962 and 1963 in Fig. 3.3 shows the powerful affect of a poor summer on

Table 3.5. Summer sunshine and temperature in 1961, 1962 and 1963.

	1961	1962	1963
April - September average temperature (°F)	47.8	45.5	46.2
July - September average temperature (°F)	51.0	48.6	49.0
July - September hours of bright sunshine	335.5	258.6	365.9

Table 3.6. Comparison of capsule formation in adjacent sheltered and exposed positions, with 95% confidence limits (after Jordan).

	sheltered position	exposed position
% of florets that have ripened to capsules	52.9±6.0	15.7±4.6
	14.9±6.0	8.2±2.1
	16.2±6.0	1.0±1.7

Table 3.7. The relation of capsules per inflorescence to summer weather and altitude, with 95% confidence limits (data extracted from Reay).

Altitude (feet)	1955	1956	1957	1958
1500	15.6±2.5	8.3±1.4	6.8±2.0	13.7
1550	13.8±1.9	9.6±1.4	2.9±2.2	8.7
1600	13.2±1.9	6.5±1.5	2.0±0.7	9.9
1650	13.2±1.9	9.0±1.2	4.6±1.9	8.8
1700	12.0±1.3	8.3±1.4	2.6±1.7	7.6
1750	17.2±1.9	8.8±1.4	5.3±1.9	8.1
1800	16.2±1.9	4.3±1.6	0.6±0.4	7.0
1850	17.4±2.4	3.6±1.4	2.0±1.9	2.8
Mean temperature (°F)	53.7	50.4	50.0	52.2
Sunshine hours	622	340	323	358

Mean temperature is the mean of the July - September maxima and minima.
Sunshine is total hours of bright sunshine.

reproductive capacity. The hours of bright sunshine and mean temperature (daily maximum + minimum meaned over the period) for the 6 growing months are given in Table 3.5. The 1962 mean was 2.2°F (1.2°C) less than the average of the last ten years, and 1.3°F (0.7°C) less than the previous lowest mean. The upper limit of capsule formation, 2925 ft. in 1961 and 1963, was forced down to just above 2300 ft., whilst the level of 25% capsule formation dropped from 2050 ft. to 1650 ft., rising again to 2150 ft. in 1963. The curves show that a few capsules are formed over quite a range of altitude down from the upper limit, then there is a fairly rapid increase to a high capsule % over an equal range of altitude. From the amount of variation shown in the graph, it seems that a similar capsule formation occurs in a very sheltered position as in an exposed position 300 ft. lower.

Jordan (1955) compared capsule formation in adjacent sheltered and exposed positions (Table 3.6), and data on capsule production contained in Reay's thesis also show the relation with summer weather (Table 3.7). The affect of increasing altitude in reducing the % of capsules can be seen in 1956, 1957 and 1958, but not in 1955, which was a very good summer.

Pearsall (1950) said fertile fruits are not usually produced above an altitude of 2500 - 2700 ft., but in 1947

Table 3.8. The number of seeds per capsule at the Moor House sites in 1962 and 1963.

Site	No. of capsules dissected 1962	No. of capsules dissected 1963	Average number of seeds/capsule 1962	Average number of seeds/capsule 1963
L	-	20		36.5
J	20	20	25.1	49.6
I	22	20	26.9	49.7
C	20	20	25.4	44.1
E	20	20	25.2	53.1
K	20	20	25.5	67.8
H	20	20	32.8	43.4
D	20	25	28.8	49.5
B	20	20	34.6	57.5
F	20		33.9	

after an exceptionally long and warm summer viable seeds were obtained from 3400 ft. on Ben Wyvis.

e) The number of seeds in the capsules

Table 3.8 compares the seed number extracted from the capsules by dissection with forceps for the different sites in 1962 and 1963. The overall average number of seeds per capsule was found to be 28.88 ± 1.8 in 1962, and 50.13 ± 2.1 in 1963. Maximum numbers were between 70 and 80. In the poor summer of 1962 it seems many more ovules failed to develop than in 1963, causing the considerable difference in the average number of seeds per capsule in the two seasons.

The capsules chosen for counting were the mature, fatter ones; in younger capsules it was difficult to distinguish the tiny seeds from the replum debris, and it was uncertain how many would develop into the larger viable seeds of the more mature capsules. But even in these there was frequently considerable variation in seed size. Jordan suggested that the seeds in some capsules would never develop because of lack of fertilisation, but in that case the capsule would probably not have formed.

In Table 3.8 there appears to be no significant difference between the sites, as a considerable amount of variation occurs between individual capsules. Reay, however, gave a table (Table 3.9) of seed weight along an altitudinal transect,

Table 3.9. The dry weight (mgms.) of seeds in capsules from different altitudes, with 95% confidence limits (mean of 6 capsules; from Reay).

Altitude (feet)	East transect	West transect
650		30.0±1.8
750		30.5±1.8
850		25.0±2.2
950		23.0±2.4
1050		27.0±3.4
1150		25.0±3.0
1250		21.0±3.6
1300		24.0±4.0
1500	18.3±2.4	
1550	21.5±3.6	
1600	16.5±2.8	
1650	18.2±1.8	
1700	20.0±3.0	
1750	16.5±2.4	
1800	16.3±2.2	
1850	13.2±2.8	

showing a small reduction in weight with increasing height. The low value for site L also points to this.

These values of seed no./capsule are somewhat higher than those in the appendices because 1) many florets classed as capsules contain only tiny undeveloped seeds when broken into and 2) the general extraction process sometimes failed to obtain all the seeds - a full dissection could not be done for each capsule because it was very time-consuming, and a more vigorous use of the forceps tended to produce debris which was very difficult to distinguish from the seeds and very tedious to separate. In 1963 so many seeds were produced that it was quite impossible to count the number in each quadrat, and the only data obtained were those in Table 3.8.

Thus 50 seeds are produced on average per capsule in a favourable season, though the actual number dispersed will be less - probably the seeds not easily shaken out by forceps would not be dispersed by natural agencies. The values given for seeds/capsule in the appendices cannot be taken as more than rough estimates of the number dispersed, but it can be said that about 10 good seeds in 1962 and 20 in 1963 would be dispersed from each capsule, and it is unlikely that this is more than twice as much, or less than half, the true number.

The values for Pendle given in Appendix 3 appear lower than those for the Moor House area, and it is possible that soil conditions or the vigour of the plant do control seed/capsule number. But the only significantly low value is 0.9 from near Lee House, Tynehead. Here there was a severe infestation of *Coleophora* larvae which had eaten the seeds (Appendix 4).

f) The effect of *Coleophora alticolella* Zell.

Pearsall (1950) described the relation of *Coleophora* to *Juncus squarrosus*, and the variations in the altitudinal limit of the moth, and two Durham students, working from Moor House, have done Ph.D. theses (Jordan, 1955 and Reay, 1958) on the moth. Three papers Jordan, 1958 and 1959, and Reay, 1964) have been produced so far, and much more information is contained in their two theses.

Life History of *Coleophora*

The moths emerge after pupation in late May or early June, and lay the eggs on the inner surface of the floret perianth segments. Sometimes the space between two adjacent florets is also utilised, especially at the higher levels where the inflorescences develop later.

The larvae usually feed on *Juncus squarrosus* seeds, but have been recorded from *J. articulatus*, *J. compressus*, *J. conglomeratus*, *J. effusus* and *J. inflexus*, and *Luzula campestris* and *L. pilosa*. In the Moor House area they frequently use J. effusus, and very occasionally Luzula campestris and Juncus articulatus. No oviposition has been observed on these last two species, and it is probable that the larvae migrate to these inflorescences from neighbouring Juncus squarrosus stems.

On hatching, the first instar larvae bore into the capsules, which by this time have mostly reached full size, especially at the lower levels. The seeds are green and soft, easily penetrable to the larvae. In favourable circumstances, with good seed-setting, the larvae pass through three instars in about six weeks, so that the fourth instar larvae usually appear in early August (but in 1954, a bad summer, they were first seen on September 14th). In capsules where the seeds fail to develop the larvae do not grow, but are still found in the early instar stages late in the season.

External larval cases outside the capsule are constructed in the late third or early fourth instar, making the infestation readily noticeable, and allowing the larvae to move to fresh capsules. There is usually only one larva in each capsule, but up to 4 have been recorded in heavy infestations. Jordan calculated that on average each larva feeds on 2.28 capsules.

The larvae overwinter in the litter in their cases, usually migrating down the culms in September after about three weeks in the fourth instar. Pupation occurs in May, though sometimes the larvae feed again after the winter, and in spring 1953 were observed on newly-developing capsules.

In 1956, Reay made frequent recordings at one station (Table 3.10), which illustrate the typical course of Coleophora infestation. The mean number of florets per inflorescence was 14.5 ± 1.6. It can be seen that capsule formation occurred between 12:7 and 26:7, egg hatching between 18:7 and 28:7, further capsule attack after the development of larval cases between 11:9 and 17:10, and larval migration between 25:9 and 12:11. It is clear that merely estimating the degree of infestation from the readily visible fourth instar larvae does not give the actual number of Juncus squarrosus seeds eaten. However, it is very time-consuming to examine all capsules for damage, and the early-instar larvae that die eat comparatively few seeds, so there is some justification for obtaining an approximate picture of the losses sustained by Juncus squarrosus from the numbers of fourth instar larvae.

Coleophora numbers and the amount of damage

Pearsall (1950) described a steady fall of infestation with increasing altitude in the Lake District. In 1942, 40% of the capsules were infested at 700 ft. (measuring by larval cases), but there was no infestation at 1800 ft. Only during the abnormal summer of 1947 did Coleophora reach higher, to

Table 3.10. Coleophora population size and capsule damage at 1500' in 1956 on the eastern transect, with 95% confidence limits. (after Reay).

date	caps./inf.	damaged caps./inf.	% cap. dam.	eggs/inf.	larvae/inf.	% larvae with cases
23:6				0.7±0.62		
26:6				1.1±0.58		
3:7				1.2±0.62		
7:7				2.1±0.78		
9:7				3.0±1.20		
12:7	0.1±0.1			3.3±1.22		
18:7	1.8±0.6	0.1±0.14	6	2.7±0.70	0.10±0.14	
20:7	2.5±1.2	0.2±0.14	6	3.0±1.10	0.15±0.14	
24:7	6.8±1.7	1.4±0.62	22	1.8±0.74	1.35±0.62	
26:7	6.8±1.5	1.6±0.54	23	1.5±0.64	1.6 ±0.66	
28:7	7.8±2.4	1.5±0.56	19	0.5±0.34	1.5 ±0.56	
3:8	10.2±1.9	1.8±0.50	18		1.8 ±0.56	
14:8	8.4±1.6	2.8±1.00	33		2.9 ±1.1	
20:8	10.6±1.3	2.6±0.56	25		2.75±0.58	
11:9	8.8±1.2	2.6±0.60	24		2.1± 0.56	14
25:9	7.8±1.4	6.0±1.22	39		2.0± 0.72	65
17:10	8.3±1.4	4.8±1.50	58		1.35±0.56	100
23:10	8.1±1.6	5.0±1.76	60		0.45±0.20	100
12:11	8.0±1.1	4.2±0.84	53		0.35±0.26	100

2000 ft. on the south-facing slope of Saddleback. In Scotland Coleophora is generally limited to lower altitudes than in the Lake District, e.g. a limit of 1400 ft. on Ben Wyvis and Rothiemurchus, and Pearsall suggests the lower mean temperature is responsible.

I have collected inflorescences from 8 localities outside the Moor House and Pendle areas, with altitudes ranging from 500 - 1500 ft., and it is interesting that Coleophora was present in all but one possibly collected before the cases were produced. On average about 5% of the capsules were infested (Appendix 4).

Jordan and Reay confined their studies to two transects. One, the western, ran up Crowdundle Beck on to Middle Tongue, beginning near Lownthwaite at 600 ft., and ending on Little Dun Fell (Jordan) and at 1500 ft. (Reay). The eastern started near Hill House in the Tyne valley, and ranged from 1500 to 2075 ft. Sampling sites were spaced at 50 or 100 ft. intervals along the transects, and Jordan took 10 or 15, and Reay 20 inflorescences.

Table 3.11 shows the number of larvae and the capsules damaged on the eastern transect in 4 different years. There was little damage in 1955, a good year for seed production (Table 3.7); more damage in 1956, when not so many capsules were produced, especially at the higher levels; very extensive

Table 3.11. Larval numbers and the amount of damage caused in the different years at the different stations, with 95% confidence limits (after Reay).

Year	1955	1956		1957		1958
Altitude (feet)	damaged cap. per infl.	larvae/ infl.	dam. cap./ infl.	larvae/ infl.	dam. cap./ infl.	dam. cap./ infl.
1500	2.1±1.2 13%	2.7±0.6	4.8±0.8 58%	a 10.8±3.2 b 4.3±1.8	6.8±2.0 100%	1.1 15%
1550	1.2±0.9 9%	1.0±0.5	2.8±0.5 29%	8.1±2.2 1.3±1.3	2.9±2.2 100%	4.9 56%
1600	1.0±0.7 7%	0.9±0.4	1.4±0.3 22%	5.4±1.5 0.6±0.5	2.0±0.7 100%	4.1 42%
1650	2.8±1.4 21%	0.9±0.4	2.8±0.4 31%	7.9±2.6 0.8±0.7	4.6±1.9 100%	4.1 47%
1700	1.4±1.0 11%	1.1±0.6	2.8±0.5 34%	5.7±1.5 0.3±0.4	2.6±1.7 100%	3.9 52%
1750	0.2±0.3 1%	0.4±0.3	1.2±0.2 14%	7.5±1.6 2.1±1.1	5.3±1.8 100%	1.8 22%
1800	0.9±0.7 6%	0.2±0.2	0.3±0.1 6%	4.6±2.0 0.4±0.4	0.6±0.4 100%	0.3 3%
1850	0.6±0.7 3%	0.1±1.4	0.0 0%	3.4±1.3 0.8±0.4	2.0±1.9 100%	0.0 0%

The %s given are the %s of capsules damaged; where two figures are given for larval numbers there was heavy mortality: - a = no. at hatch, b = no. 20 days later.

damage in 1957 when large numbers of eggs were laid, but very few inflorescences developed (Table 3.2) resulting in severe overcrowding of the larvae; and little damage in 1958 as few larvae survived. Thus the amount of damage to the capsules depends both on the number available, and the size of the *Coleophora* population in the year.

Observations in 1962 indicate that in a bad summer larval development is so slowed that many never reach the fourth instar before the winter, and consequently much less damage is done. The first larval cases were seen on 1:10 in the populations from the Dipper to the Tyne source (1550 - 1750 ft.) and on 26:10 both third and fourth instar larvae were present in the cases.

As almost all the seeds in a capsule are spoilt, if not eaten, *Coleophora* infestation can reduce the *Juncus squarrosus* seed production at some levels to practically nothing in some years. The average production may well be reduced by a third below 1500 ft.

The altitudinal limit of *Coleophora*

The highest stations of successful larval development and seed-setting in a particular year are shown in Table 3.12. The slow upward dispersal after a fall is due to the relatively inactive life of the adult.

Table 3.12. The altitudinal limit of _Coleophora_ (partly after Jordan and Reay), giving
a) upper limit of successful larval development in a season
b) upper limit of seed-setting in the season
c) average mean temperature from April to July.
altitudes in feet, and temperatures in degrees Fahrenheit.

East		1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963
a)	larvae	2000+	2170	1850	1850	1850	1800	1800	-	-	1700	1700	1650
b)	seed	2500+	2500+	2100	1850‡	1850+	1850+	1850+	-	-	2925	2300	2925
c)	temp.	47.1	46.6	45.4	46.6	45.6	46.5	45.3	47.6	47.8	46.1	44.4	45.3

West							
a)	larvae	1850	1850	1400	1450	1500	1500
b)	seed	2500+	2500+	1400	1500‡	1500+	1500+

\+ indicates above this height ‡ indicates well above this height.

Pearsall put forward two explanations for the limit:-

1) Life cycle not coincident with flowering - no florets when the moths emerge, preventing oviposition at the limit.

2) Egg and larval development controlled by the temperature, so that larvae cannot move to the litter before the end of the season at the limit.

He favoured the former, because at the higher levels only the early ripening capsules were infested. The 1962 observations have some bearing on the second factor. Fourth instar larvae were still present on the florets in December, when very severe weather set in, but after the snow cleared in April 1963 some were found to be still alive. On 16:5 further inflorescences were collected, and the number of cases per inflorescence appeared less. One larva with a case was seen on a stalk, probably migrating. In autumn 1963, however, larvae were found almost up to the same levels as in 1962, the imagoes presumably having emerged at the usual time despite the delayed larval development.

Jordan, because of the 1954 results, said the limit was controlled by seed-setting, which is governed by the weather and especially the mean temperature. Reay agreed, but also showed that the alternative host of Juncus effusus could prevent extinction of Coleophora when the food supply of Juncus squarrosus failed in 1957. Despite no larvae reaching the fourth instar on Juncus squarrosus on the eastern transect, some that fed on J. effusus were able to provide a small population of normal moths next season at all but the highest station of 1850 ft.

Therefore it would seem that any of these three factors can cause extinction of Coleophora near its upper levels. The multiplicity of controlling factors is really to be expected in dealing with a marginal population. It is advantageous to Juncus squarrosus that other factors beside its seed production can reduce Coleophora infestation. Thus there is good seed production in most years over a range of two or three hundred feet between the upper limits of sizeable Coleophora population and general capsule ripening.

g) The resulting seed production

Whilst in places the various factors governing seed production tended to balance each other, there was in 1962 a substantial difference between 415 seeds/quadrat at Dipper - F (1550 ft.), an average of about 100 seeds/quadrat around the 1800 ft. contour, and 5 seeds/quadrat at 2300 ft. Seed production was probably at its maximum in 1963 - taking averages of 20 inflorescences/quadrat and 5 capsules/inflorescence (see Table 3.1) and 20 seeds/capsule (see p. 3.15) gives a production of 2000 seeds per quadrat. If such favourable seasons were to continue, Coleophora would move up the fell, counterbalancing the rise in production.

Pearsall writes that 'the amount of inflorescence growth, and the production of flowers or better still of fruit and seeds, both diminish as the altitude increases' and illustrates by a graph with three very straight lines. He neglects the affects of Coleophora attacks at the lower levels, and of soil conditions and the plant's vigour. By their control of the floret/inflorescence and inflorescence/quadrat ratios, these two factors affect the seed production considerably, within the major limit set by increasing altitude on capsule formation. Thus favourable soil, together with a particularly favourable micro-climate, led to a value of 177 seeds per quadrat at site C in 1962, there being a high florets/ inflorescence ratio. Site I with young vigorous plants on a not very favourable soil, had a value of 105 seeds per quadrat chiefly because it had a large inflorescence/quadrat ratio. Of the mid-altitude sites, J had the second highest figure of 132 seeds per quadrat, having fairly high values for both inflorescence/quadrat and florets/inflorescence. Juncus squarrosus has a high degree of dominance in this community, and the wet conditions favour its growth.

It is clear that each year Juncus squarrosus produces enormous amounts of seed on the northern Pennines. At the maximum value of 2000 seeds/quadrat (8000/sq. m.) there would be 1600 million seeds produced per square mile, even if *Juncus squarrosus* communities only occupied one tenth of the area. In most years something near to this maximum value will be produced between 1500 and 1800 ft, though below this level *Coleophora* attack will reduce the average. At the higher levels the low seed/quadrat values will be partly balanced by the greater extent of *Juncus squarrosus* communities - they occupy up to a third of some square miles. Even at 5 seeds/quadrat, an acre of *Juncus squarrosus* will produce 80,000 seeds. But above 2500 ft. a substantial seed production will only occur infrequently.

B) SEED DISPERSAL

The seeds of _Juncus squarrosus_ are very small, and are dispersed by the wind. A week or so after the seeds have ripened, the capsule segments open, allowing the seeds to be blown out. This is very much aided by dry conditions; otherwise the capsules hold water and the surface tension prevents dispersion.

At Moor House in 1963 there were open capsules in August at 1550 ft. (site F), but at 1850 ft. very few capsules had opened by the end of September. However, by spring most of the seeds had been dispersed from capsules below 1800 ft. (Table 3.13), though above this level many capsules were still unopened. These probable remain closed and give rise to the groups of seedlings found at the ends of old fallen inflorescences. As a result the number of seeds dispersed at the higher levels must be considerably reduced.

Samples were taken of the peaty material which becomes apparent on the top of snow at Moor House during times of thaw. A few seeds of _Juncus squarrosus_ germinated, but no other species was found. Thus _Juncus squarrosus_ seeds can survive dispersal with drifting snow.

Pearsall (1950), seeking to explain the occurrence of _Juncus squarrosus_ on the highest mountains above the level of normal seed-setting, suggested that the fruits might be

Table 3.13. The number of seeds in the capsules at site B in autumn 1963 and the following spring (with 95% confidence limits).

Date	Seed number
10th September, 1963	57.5±6.98
13th May, 1964	13.1±6.95

distributed in the wet wool of sheep. While this may occur on occasions, sheep cannot be an important agent of dispersal. The inflorescence is too strong for pieces to become detached onto the fleeces of passing sheep, and it is very unusual to see a broken inflorescence or one with capsules missing. He suggested too, that snow buntings (*Plectrophenax nivalis*) disperse the seeds by eating the capsules. At Moor House grouse (*Lagopus scoticus*) also eat the capsules, as they have been found in dissected crops amongst the many heather shoots, and at the few sites where inflorescences had lost capsules, grouse droppings were noted closeby. But even if the seeds in the droppings can germinate, there are so few snow buntings, and grouse eat the capsules so infrequently, that neither agency is important in comparison to the wind.

There is no information available on the longevity of *Juncus squarrosus* seeds, but Becquerel (1907) said *Juncus articulatus* seeds had survived for 65 years, and *J. bufonius* seeds were also very long-lived. Shull (1914) reported that *J. bufonius* and *J. tenuis* seeds germinated after being kept in water for 7 years. A considerable literature exists on the occurrence of buried viable seeds. Chippindale and Martin (1934) showed the greatest density of viable seeds of *Juncus squarrosus* (and many other species) was in the top 3 in. (8 cm.) of the soil. Viable seeds were obtained up to 7 in. (18 cm.) below the surface, but this does not necessarily mean that they have survived for a long period, as their small size allows them to pass rapidly down the soil.

Milton (1936) showed the presence of seeds of Juncus squarrosus in soils from very varied vegetation in Wales. In some cases samples were taken several miles from the nearest stands of Juncus squarrosus, so that either the seeds had been wind-borne or had survived since Juncus disappeared on pasture improvement. Table 3.14 shows the frequency of its seeds occurring in the soil samples, and their maximum density in a sample. A further paper (1939), describing transects up Plynlimmon and Cader Idris, showed that the seeds are most frequent in the soil when Juncus squarrosus is well represented in the sward above.

Champness and Morris (1948) did not find Juncus squarrosus seeds at any station below 1000 ft., though viable seeds were obtained from 10 out of 12 fields examined above this level. They recorded 18.77 million seeds/acre (7.6 million/ha.) in one field, the maximum density reported in this literature. The usual density is between 1 and 5 million seeds/acre.

Thus seeds of Juncus squarrosus are effectively dispersed for medium distances of up to a few miles, and large numbers are present in the soil ready to germinate when conditions are favourable.

Table 3.14. The frequency of viable *Juncus squarrosus* seeds in soils from a variety of habitats in the Welsh uplands, (after Milton).

Habitat	Number of samples	Samples with Js.	Maximum population (in millions of seeds/acre)
1 to 5 yr. old leys	16	2	0.1
Older leys	14	4	1.12
Festuca - *Agrostis* dry grassland on hill slopes	39	17	3.37
Hill slopes with *Molinia*, *Nardus* and *Festuca*	13	12	7.75
Open hill with marsh of *Molinia*, *Juncus*, *Trichophorum*, Carices, *Calluna* and *Narthecium*.	12	10	10.82
Similar marsh enclosed	7	7	15.70
Woodland, 13 yr. old	9	6	0.82
Former arable fields	14	5	1.70

C) SEED VIABILITY

Trials have been made of the seeds produced during the three fruiting seasons at the different sites used to measure reproductive capacity. Several different media were used, and the results of these comparisons are dealt with in the next section, together with the conditions necessary for germination.

Difficulties arise in dealing with tiny seeds such as Juncus squarrosus, because the less-developed are not easy to distinguish from replum debris (as mentioned on p. 3.14). But the seeds used in these tests were in all cases of the same nature as those counted as seeds in the measurement of the number of seeds per capsule. Unfortunately, no trials were done to relate viability to seed size; difficulties of measurement and handling would have been great, and there is also the possibility that very tiny seeds would have tended to wash down into the soil, giving a lower germination %.

Hence, these trials show what proportion of the measured seed production would germinate, if dispersed to a suitable habitat.

Methods

Packets of 50 seeds (100 in 1961), representing the different quadrats or samples collected from a site, were obtained as described on p. 3.4 . They were stored in a dry, dark place until the day of sowing, which was 28th November in 1961, 20th December in 1962 and 10th December in 1963.

The pots or tins (their preparation is described in section 4) were placed on the shelf of a south-facing window inside Moor House, where the temperature rarely fluctuated outside the range 50-58°F (10-15°C), 55°F (13°C) being the average. Watering was frequent; and during the last two years the pots were kept in standing water to keep the media reasonable moist at all times. Counts of the number of seeds which had germinated were made every 3 or 4 days. This was necessary as sometimes a seed would germinate, and then the tiny seedling die and disappear, so that germinations would go unrecorded if longer periods separated seed counts.

Occasionally the pots were moved around as it was possible that there would be a higher light intensity but a lower temperature close to the window.

In 1961-2, some germination trials were done in a slightly-heated greenhouse at the Science Laboratories in Durham. The environment was more humid and lighter, though cooler than at Moor House, but as the final germination percentages were similar, both series of results have been treated as one.

Recording was continued till about midsummer, when the number of fresh germinations became very small.

Table 3.15. Comparison of seed viability of plants of *Juncus squarrosus* on peat and mineral soils in 1961, shown as % germination.

Altitude up Tees transect (feet)	Alluvial mineral soil	Peaty podsol or gley
1750	81	78
1975	69	70
2250	58	55

Table 3.16. The seed viability at different altitudes in 1961.

Altitude of stand (feet)	1400	1750	1975	2250	2500	2650	2725	2925
No. of samples of 100 seeds tested	2	20	9	7	3	1 of 30 seeds,	9 and	1 seed
% germination	89	80	69	57	39	3	0	0

Results

a) Seed viability of plants on different soils at the same site

In 1961 inflorescences were collected at 1750 ft., 1975 ft. and 2250 ft. in the Tees Valley from stands on the alluvial terrace and on a peaty podsol or peaty gley closeby. No significant difference was found in the viability of their seeds, as shown in Table 3.15. The results in this and the remaining tables in this section are averages of trials on all media.

b) Seed viability in the different seasons, and at different altitudes

A very high proportion of the seeds produced in 1961 were found to germinate, as shown in Table 3.16. The percentage fell above 1750 ft., but even at 2500 ft. almost half the seeds germinated, and there was 1 germination from the 30 seeds obtained at 2650 ft. The capsules at 1400 ft. were infested by Coleophora, but this has not affected the viability of the seeds.

In Table 3.17 seed viability on Pendle Hill is given for the 1961 season. The plants from 1150 to 1550 ft., which were poorly grown and produced few seeds, had also poor seed viability. In this instance soil conditions are having an effect, but by lowering the vigour of the plants, in contrast

Table 3.17. A comparison of seed viability in 1961 at different altitudes on Pendle Hill, Lancs.

Altitude in feet	Number of sites	Germination %
950	1	88
1150 - 1550	3	56
1750 - 1830	2	99

Table 3.18. A comparison of the seed viability in 1962 and 1963 at the 12 sites at Moor House (with 95% confidence limits).

Site	Altitude in feet	1962	1963
G	2925	0	0
A	2450	0	0
L	2300	0	0.5± 0.8
I	1900	20.0±9.1	18.2±12.4
J	1900	6.2±2.2	18.5±16.8
K	1850	6.0±4.9	44.8±21.0
E	1850	10.0±13.9	29.6±16.0
C	1850	18.4±3.0	31.2± 9.3
H	1800	10.8±4.6	41.6±19.7
D	1775	15.0±4.4	38.2±18.7
B	1750	13.6±2.3	41.6±11.8
F	1550	8.5±1.7	53.6± 2.1*

* - from experiments described in section 4.

to the Tees plants which were equally well-grown on the different soils.

Whilst 1963 did not produce as high a percentage of viable seeds as 1961, it was considerably better than 1962. Table 3.18 compares these two years at the 12 Moor House sites. Most of the values are averages of 10 trials, seed for each coming from an adjacent pair of quadrats.

No relation can be established between the sites and their seed viabilities in the different years. In 1963, increasing altitude between 1750 and 1900 ft. seems to have an important effect, but this was not so in 1962. Considerable variability was found between the different quadrats at a site, resulting in the large confidence limits.

It is interesting that despite 19% of the florets being apparently ripe (Table 3.1) at site L in 1963, so few of the seeds were viable. In 1962 there were fewer ripe capsules at the lower levels, yet they contained a higher percentage of viable seed. It would seem that some time elapses between the capsules becoming apparently ripe and the seeds becoming viable.

SECTION IV: GERMINATION AND THE FACTORS WHICH AFFECT IT.

The section opens with a brief illustrated description of the germination. An account follows of the necessary conditions for germination and the effects of the various factors on its rate.

Germination

The seeds of Juncus squarrosus are brown or yellow-brown, very small and very light, with an average weight of 0.0275 mg. (Dallmann, 1933). Very few plants have seeds with weights less than this; they include J. bufonius (0.015 mg.) and Sagina apetala (0.0075 mg.). The Juncaceae belong to the Rudimentary - Broad division in the seed classification of Crocker and Barton (1953), with relatively small embryos, which are broad and peripheral, and have starchy albumen. Laurent (1904) said the albumen was soon used up, and gave some illustrations of the early stages of germination.

Germination is epigeal, as shown in Fig. 4.1, and similar to Juncus effusus and J. conglomeratus, figured by Richards and Clapham (1941) in the Biological Flora. The cotyledon base emerges first and curves down to the soil, becoming attached by a circlet of root hairs. Chlorophyll is apparent a day or two after germination has begun. The cotyledon base now straightens and elongates, carrying the seed up on its tip. After about a fortnight the first lateral leaf appears.

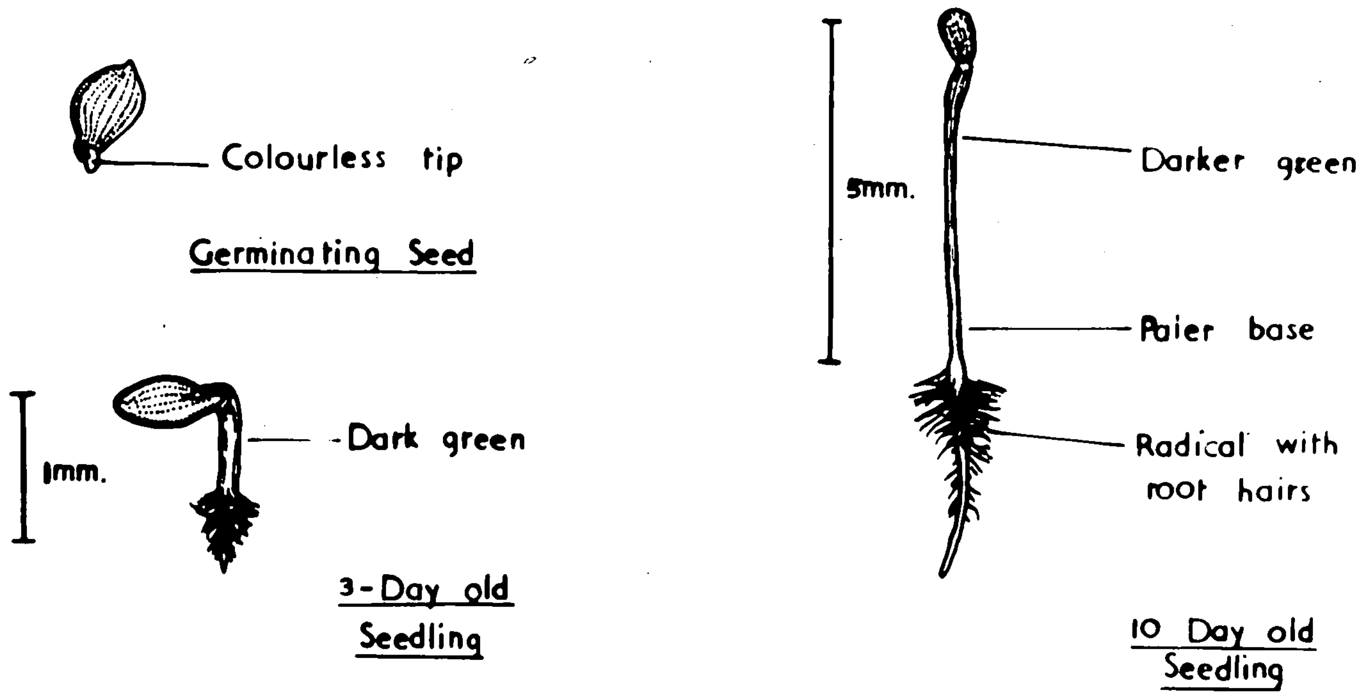


Fig. 4·1. The germination of *Juncus squarrosus.*

Juncus squarrosus is a spring germinator, though some seeds germinated indoors as early as September. It seems that the seeds will germinate at any time from shortly after dispersal if the conditions are suitable. In 1962 seedlings in the field were first noticed on 27th May, and had probably germinated about 10th May, the cool weather no doubt causing slow growth.

Factors which affect germination

1) Position of seeds

An experiment was done in Autumn 1961 to compare the germination of seeds sown on a peat surface with those buried from 1/4 to 1/2 in. below. No germination of buried seed occurred, and in all further trials seeds were sown on the surface.

2) Substrate

Methods

Four media:- calcareous drift, acid drift, humified blanket peat and fabric over water have been used during the course of the work. The fabric (Curlene M 104) was placed in beakers, but the three soils were either in clay pots or aluminium soil sample tins, both 2½ in. in diameter. The soils were obtained from the same sites throughout the work, and after drying indoors were mixed until homogeneous. The calcareous drift, of pH 7.0, came from over the Tyne Bottom Limestone in

Table 4.1 The germination percentages on different media (significant difference at 5% level is starred)

		Media				
Year	number of comparisons	Fabric	Peat in tins	Acid drift in tins	Acid drift in pots	Calcareous drift in tins
spring 1962	9	83*	77			65*
	12	82	69			
	4		83	71		59
spring 1963	8				17	13
	15		7		12	

the pasture by Moor House, the acid drift (pH 4.7) from over the sandstone outcrop by Nether Hearth Sike just in front of the meadow, and the blanket peat (pH 3.3) from eroding haggs just behind the house.

The soils were packed firmly into the tins or pots above crocks at the base, and the surface smoothed, as any cracks or irregularities would allow the very light seeds of Juncus squarrosus to wash away. Watering was done gently, and at regular intervals. Tins were used in the early experiments as drying out occurs less rapidly from them than clay plant pots, and Juncus squarrosus seedlings seemed not to suffer in any way from growing under permanently waterlogged conditions. But later, clay pots immersed in a water bath were used; this reduced the amount of watering needed. The experiments were conducted in Moor House as described on p. 3.29.

Results

The greatest germination percentages (Table 4.1) were obtained on the fabric, probably because no seeds were lost by being washed down into the soil. But this medium was abandoned after the first year because the roots could not penetrate the fabric mesh (a coarser mesh allowed the small seeds to fall through). Hence the seedlings were unable to establish themselves and straggled, making counting very difficult.

The only significant difference at the 5% level is that between the fabric and the calcareous drift in 1962, but it does seem that the germination percentages are rather lower on the calcareous drift than on the peat and acid drift. Accordingly, in 1964 all the germination trials were done on peat in tins (light experiments) or pots (site viability trials).

Thus the differences between the media are not great, and do not mask the differences between the years. Hence in the comparisons of viability between habitats and seasons, all trials on the different media have been treated together.

Discussion

The lower germination on the calcareous drift fits with an observation by Pearsall (1949) that a higher pH appears unfavourable to germination. In some small-scale experiments, he reported a 25% germination on a fen peat of pH 6.5, but no germination on a marl of pH 7.6. No critical experiments have been done in the present work on the relation of germination to pH, but it seems that reasonable germination would occur on all soils which Juncus squarrosus seeds reach in upland areas, as very few are even neutral at the surface. It would thus appear that factors other than the nature of the soil are preventing the germination of Juncus squarrosus in the better swards at Moor House.

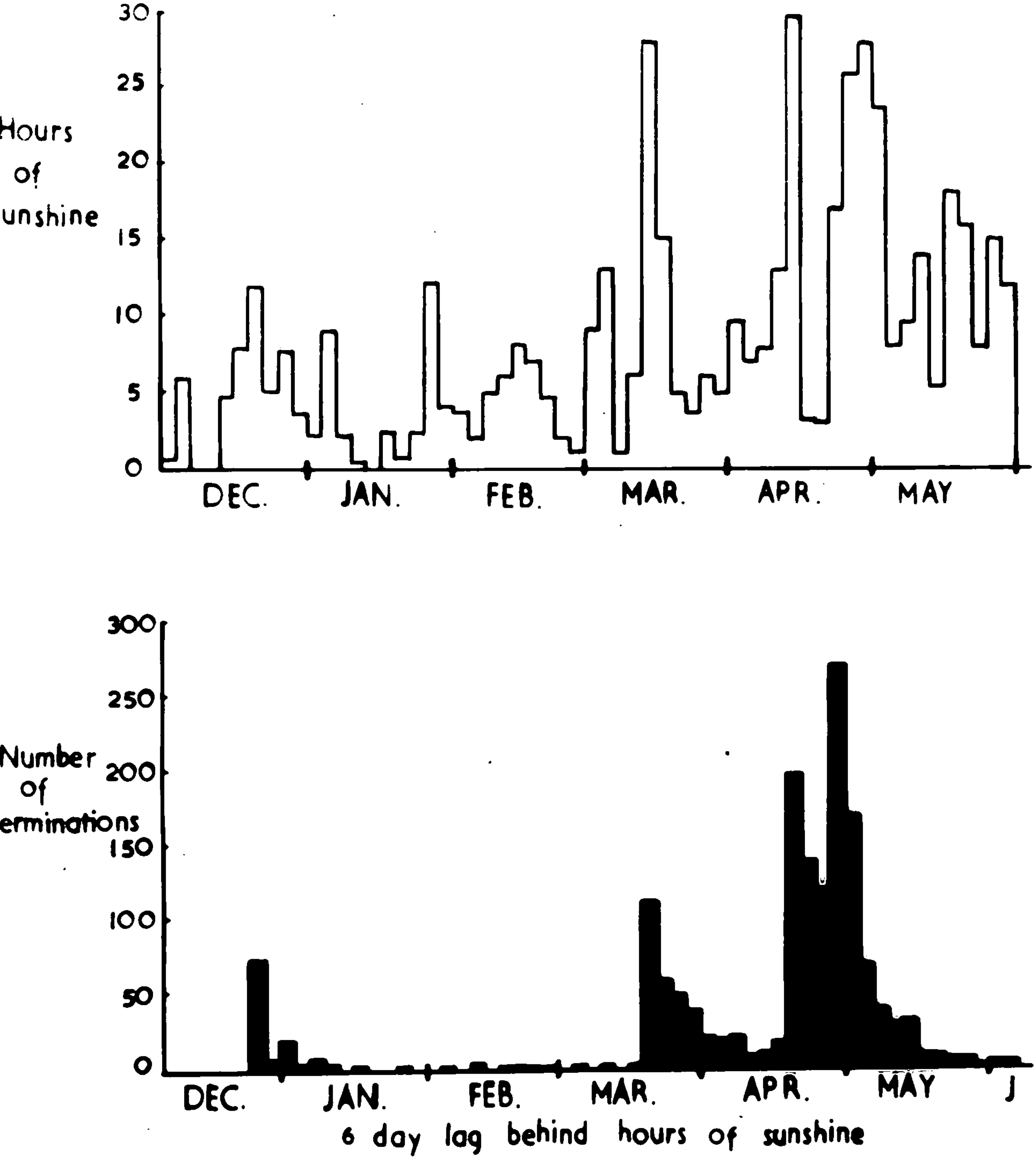


Fig. 4·2. The relation of germination to sunshine hours in 1962.

3) Light

Richards and Clapham (1941 and 1943) reported that at least five *Juncus* species (*J. effusus*, *J. inflexus*, *J. macer*, *J. subnodulosus* and *J. filiformis*) require light for germination. Accordingly, the relationships between germination and the duration and intensity of light have been investigated.

A) Sunshine hours and germination %

The number of seeds germinating in the seed viability trials during 3 or 4 day periods was compared to the hours of bright sunshine recorded at Moor House during the previous few days. Most of the sunshine received during the time the trial was in progress reached the pots and tins on the window-ledge in Moor House.

In 1962, there was a fairly good 'trigger-action' relation between the number of seeds germinating in a 3-day period, and the hours of sunshine received in an equal period 6 days previously, as shown in Fig. 4.2. Three sudden peaks are seen - on 21st March, 20th April and 29th April - followed by a steady reduction in the number germinating, and these peaks are parallelled by high sunshine totals on 15th March, 14th April and 23rd April. The 26th April sunshine total is higher still than the 23rd, but on this occasion the number of germinations was less on 2nd May. Perhaps by this time the lag between the sunshine being received and the seeds germinating had been reduced, but the more likely explanation is that there were only a few seeds still to germinate.

In the 1963 seed viability trials in the same position, a double peak of germination was recorded, but there was no good correlation with sunshine hours. It is possible that the room temperature in Moor House was controlling germination more than sunshine hours in this instance, as germination did not occur at the end of February when there was a good sunny, though very cold spell of weather. The first peak came on 5th April, when the previous sunshine had been only average in amount, but the second peak on 4th June did correlate with a sunshine peak on 29th May.

Work described in the next part shows that in constant conditions there is a sudden sharp peak followed by a steady fall in the number of seeds germinating. Thus double- or triple-peak germination is not an intrinsic feature of the seeds of *Juncus squarrosus*, but a result of change in the external conditions.

B) The relationship between light intensity, duration and germination %

Five experiments were done in Autumn 1963 and Winter 1964 using seed from a single source (Dipper - site F). 50 seeds were sown per tin on to the peat medium previously described.

The light intensity was varied by having 2 shelves at different levels and by covering groups of tins with perforated zinc sheets. The experiments were conducted in 2 places with differing conditions:-

A) A growth room in the Science Laboratories at Durham, with a constant temperature of 73°F (23°C), and fluorescent lighting. The temperature at shelf level rose by 2°F (1°C) when the light was on.

B) An improvised growth room in Moor House, with ordinary tungsten filament lights and with an average temperature of 57°F (14°C), fluctuating normally within the range 55 to 59°F (13-15°C). A thermograph was run throughout, and showed extremes of 52°F (11°C) and 66°F (19°C). It was also found that the temperature at shelf level rose by 4°F (2°C) when the light was on, but it took at least 2 hours before the maximum level was reached, and with a 1-hour light day the effect on temperature was hardly detectable. The room temperature also increased, but only by 2°F (1°C).

Experiments 1, 2 and 5 were done in Durham, with 12-hour, 1-hour and 12-hour light days respectively. Experiments 3 and 4 were done at Moor House with 8-hour and 1-hour light days respectively. Experiment 5 was done to show the effect of the normal winter conditions at Moor House on the subsequent germination of the seeds, and is described on p. 4.11.

Table 4.2. Comparison of germination %s at 73°F (Durham) under different light treatments. (with 95% confidence limits).

a) 12 hours of light per day

Intensity of illumination (foot candles)	Days from start of trial: 13	21
Strong	47.0± 4.8	53.6± 2.1 overall average (Strong, Medium, Weak, Very weak)
Medium	61.5±12.3	
Weak	47.5±15.0	
Very weak	63.0±16.1	
No light (average of 2 tins)	5.0	32.0

b) 1 hour of light a day

	Days from start of trial: 13	21	31
Strong	35.4±14.0	41.8±17.8	43.5±16.9
Medium	45.5±28.6	48.0±31.6	49.0±30.8
Weak	14.5±12.4	20.5±18.6	27.0±30.7
Very weak	13.5± 7.0	19.0±10.2	27.5±10.5
No light (average of 2 tins)	13.0	20.0	24.0

Table 4.3. Comparison of germination %s at 57°F (Moor House) under different light treatments. (with 95% confidence limits).

a) 8 hours of light per day

Intensity of illumination (foot candles)		Days from start of trial: 13	21	31
Strong	20.0	37.1 ± 2.3	55.5 ± 2.8	57.5 ± 4.2
Medium	10.0	25.0 ± 8.5	44.5 ± 4.6	51.0 ± 2.8
Weak	6.5	24.5 ± 12.5	45.5 ± 5.4	54.0 ± 4.1
Very weak	2.5	17.5 ± 9.0	30.0 ± 7.8	39.5 ± 7.8
No light (average of 2 tins only)		0	0	0.5

b) 1 hour of light per day

Intensity of illumination (foot candles)	Days from start of trial: 13	21
Strong	1.5 ± 4.8	32.0 ± 17.0
Medium	1.0 ± 1.8	17.5 ± 12.0
Weak	0	12.0 ± 9.4
Very weak	0	8.5 ± 10.2

Results

Tables 4.2 and 4.3 show the considerable effects of different light treatments on germination. Confidence limits are unfortunately high - probably 4 tins per treatment was insufficient. At 73°F (23°C) in Durham, a 12-hour light day resulted in the rapid germination of seeds at all intensities of illumination, and little germination occurred after the thirteenth day. But germination was slower when only 1 hour of light was given per day, especially at the lower intensities, and even after 31 days only half the viable seed had germinated in these tins. It is interesting that at this temperature germination occurred in the control tins receiving no light, though at a slower rate than in the tins receiving only very weak light.

There was slower germination in the third and fourth experiments at Moor House, where the temperature was nearer to that obtaining in the natural environment when the seeds are germinating. The slow rate was most marked (Table 4.3) at the lower illumination intensities and in the one hour of light per day treatment. In this very few seeds had germinated after 13 days in contrast to all other treatments, and many viable seeds had not germinated after 21 days even in the strong light intensity.

Table 4.4 Germination numbers in 3 or 4 day periods of experiments in which the tins were moved from one light treatment to another. The totals for the treatments marked (x) have been doubled, as only two tins had this, other treatments being given to groups of four tins.

a) 1 hour of light per day at 73°F (Durham)

First treatment	Number of germinations	Second treatment	Day number from start of second treatment: 2	5	9	12	16	19	23	Total Germinations	
Strong light for 8 days	52	No light (x)	2	8	0	0	0	0	2	14	=66
	46	Very weak light	7	8	7	5	4	0	0	31	=77
	68	Strong continued	9	9	5	0	3	0	0	26	=94
Very weak light	15	V.weak continued	8	5	7	4	8	2	7	41	=56

First treatment	Number of germinations	Second treatment	2	5	9	12	16	Total Germinations	
Strong light for 15 days	86	Strong continued	5	0	3	0	0	8	=94
	70	No light (x)	6	2	0	0	0	8	=78
	71	Very weak light	2	3	2	1	1	9	=80

b) 8 hours of light per day at 57°F (Moor House)

First treatment	Number of germinations	Second treatment	Day number from start of second treatment: 1	5	9	13	17	20	24	Total Germinations	
Strong light for 8 days	6	No light (x)	20	24	4	4	2	2	2	58	=64
	7	Very weak light	10	51	5	13	9	4	4	96	=103
	6	Strong continued	35	42	15	13	0	4	0	109	=115
Very weak light	0	V. weak continued	3	32	17	8	9	8	2	79	=79

First treatment	Number of germinations	Second treatment	3	7	11	14	18	Total Germinations
Strong light for 14 days	83	Strong continued	15	13	0	4	0	32=115
	68	No light (x)	8	4	12	0	0	24=92
	71	Very weak light	16	12	7	0	0	35=106

C) The mode of action of light

In the first three experiments an attempt was also made to find out whether light acts as a trigger in starting germination, or whether its presence is necessary during the time of germination. In each experiment there were 12 additional tins besides those being used to show the effects of intensity of illumination, and these received strong light. After 8 days, 6 of the tins were moved into very weak light (4 tins) and total darkness (2 tins), and the other 6 tins were likewise moved after 14 days.

Germination was significantly reduced in the tins put into total darkness after 8 days, as seen in Table 4.4, and there was also a slight reduction in the number that germinated in tins placed in darkness after 14 days. In very weak light the final total of germinations was the same as under strong light throughout, and greater than in tins kept in very weak light throughout. However, some delay in germination was apparent.

From these experiments the following conclusions can be drawn:-

1) Light does not solely have a trigger-action.
2) Light during the time of germination increases the rate and final total.

Table 4.5. Germination percentages of seeds receiving one hour of light per day at different temperatures, with 95% confidence limits.

Intensity of illumination	73°F (Durham) after 13	20 days	57°F (Moor House) after 13	20 days
Strong	35.4±14.0	41.8±17.8	1.5±4.8	32.0±17.0
Medium	45.5±28.6	48.0±31.6	1.0±1.8	17.5±12.0
Weak	14.5±12.4	20.5±18.6	0	12.0± 9.4
Very weak	13.5± 7.0	19.0±10.2	0	8.5±10.2

3) Both increased intensity of illumination and longer light days assist germination.

4) The effect is cumulative as the total number of germinations is related to the total amount of light received.

4) <u>Temperature</u>

The effects of temperature will already be apparent from the results given above. The germination rates at the different temperatures under the same light treatment are compared in Table 4.5. Higher temperatures give faster germination and minimise the effects of low intensities of illumination. At 73°F it is clear that the heat is performing the same function in the process of germination that light does at lower temperatures, as germination even occurred in the dark.

At Moor House the controls of the third experiment, in which only one seed germinated on the 30th day, and the tins which received very weak light, were given a strong intensity of illumination in the fourth experiment which followed immediately. Very soon further germinations occurred, but it was 12 days before any germinations were recorded in the other tins receiving this light treatment (Table 4.6). Thus it seems that even at 57°F, temperature can have the same cumulative effect as light when the seeds are in a receptive condition.

Table 4.6. Germination numbers in 3-day periods of experiments in which the tins were moved from darkness or very weak illumination into strong illumination, as compared with the numbers in controls receiving strong illumination throughout.

First treatment 8 hours per day	Number of germinations	Second treatment 1 hour per day	Day number from start of second treatment							Total Germinations		
			3	6	9	12	15	18	21			
No light for 31 days	2	Strong light	4	4	26	32	8	18	6	98	=	100
Very weak light for 31 days	79	Strong light	3	1	1	0	1	1	0	7	=	86
None	-	started in strong light	0	0	0	3	16	34	11	64		64

It is probable that germination cannot take place below a certain temperature even when light and substrate conditions are suitable. No work has been done on this, but a close watch was kept for the first young seedlings appearing out of doors in 1962. None were seen till late in May, and allowing for a slower growth rate outside than in the warmer environment of Moor House, it was calculated that these seeds germinated about 10th May. Night minima were then about 40°F (5°C) for the first time that year, and day maxima averaged 55°F (13°C).

The final trial done in Durham in Spring 1964 (Table 4.7) showed that subjecting the seeds to winter conditions at Moor House - for most of the three winter months the seeds and peat substratum were frozen - had no appreciable effect on the germination % or rate. The slight fall in numbers germinating may well be due to some seeds being buried by movements of the peat. The ability of seeds to germinate in the dark at the high temperature (73°F - 23°C) of the trial was also unaffected.

5) Other factors

In 1961 both dilute KNO_3 and alternating temperatures (warm in the day, and cold at night) were applied, as Crocker and Barton (1953) stated that they improved or stimulated the germination of light-sensitive seeds. Each treatment was given to 2 tins, but no effect was detectable, similar germination %'s being obtained as under normal conditions.

Table 4.7. Germination %s of seeds sown in autumn given light and warmth immediately, and given light and warmth in the following spring after being subjected to outside conditions at Moor House. (with 95% confidence limits).

	Autumn germination	Spring germination
a) at various light intensities		
after 11 days	49.6±2.1	43.0±6.8
after 16 days	51.8±2.1	44.2±7.2
b) control with no light		
after 11 days	1.0	7.0
after 16 days	12.0	9.0

Pearsall (1949) reported that freezing before sowing raised the germination % of seeds on _Eriophorum vaginatum_ peat of pH 3.3 from 5 - 10% to 30%, but had no effect when the substrate was _Sphagnum_ peat of pH 4.0. This, however, was a small experiment, and the results may well have been due to chance.

Under natural conditions, seeds of _Juncus squarrosus_ will nearly always experience frost before conditions are suitable for their germination. In the Moor House area the seeds were frosted before they were collected from the capsules, and therefore freezing treatment has not been investigated.

The sensitivity of the seeds towards root exudates that inhibit germination has not been determined. Osvald (1949) reported that rape seeds would not germinate in an extract from a soil in which _Festuca rubra_ had been growing, though they germinated readily in extracts from soils in which there had been no _Festuca_. It is just possible that this is the explanation of the failure of _Juncus squarrosus_ seeds to germinate in grass swards even when they are grazed down, allowing a fair amount of light to reach the soil surface.

Discussion

For many years studies have been made on the factors controlling germination, especially that of light. Kinzel as long ago as 1917 said 'Light and dark play an important part in the germination of seeds in nature, and different reactions in this respect are to be regarded as a response to environmental conditions.' Thus germination in different species may be light-hindered, light-aided or light-indifferent according to their environment.

Mayer and Poljakoff-Mayber (1963) have produced a good account of the factors affecting germination, and discuss their value to the plant. Light requirement has frequently been associated with small seed size, as it is thought necessary for photo-synthesis to produce more food substances shortly after germination has occurred. But they point out that what is important is the ratio between the amount of stored materials and the size of the seedling to be nourished by them. However, it is probable that this is low in Juncus squarrosus, in which case light sensitivity would be advantageous to the plant, preventing the wastage caused by seeds germinating where and when conditions are unsuitable.

Mayer and Poljakoff-Mayber also give an account of the effects of light of different spectral lengths on germination. Red light often promotes germination, but blue is inhibitory. However, the fluorescent light used in the 3 Durham experiments had no such effect on the seeds of Juncus squarrosus.

Temperature and the acidity of the substrate often profoundly influence the effect of light in the germination of light-sensitive seeds. Some germinate in the dark at suitable temperatures if provided with an acid substrate, and it is clear that *Juncus squarrosus* belongs to this category, though it is not known whether germination also occurs in the dark on a neutral medium.

Ottenwälder (1914) showed this effect with many small seeds including *Lythrum salicaria*, *Verbascum thapsiforme*, *Scrophularia nodosa* and *Oenothera biennis*. Results for *Lythrum* are given in Table 4.8; these differ from those for *Juncus squarrosus* only in the higher temperature needed for germination in the dark. With *Oenothera biennis*, there was a very high dark germination at 79°F (26°C), but only 3% at 73°F (23°C).

It is now generally assumed (Mayer and Poljakoff-Mayber) that light acts as a catalyst in a photochemical reaction which initiates a series of reactions leading to germination. This theory explains the variation in germination rate of *Juncus squarrosus* seeds in different light and temperature conditions. Only at high temperatures does the photochemical reaction proceed sufficiently fast for light to be unnecessary. At lower temperatures the reaction only proceeds when light is present, explaining its cumulative effects and why further germination is stopped after light has been removed, the substance produced having been used up.

Table 4.8. Germination of Lythrum salicaria under controlled conditions. (after Ottenwälder).

Days from sowing	Temperature 23°C light	23°C dark	30°C light	30°C dark
2	41%	0	98.5%	0
3	95.5%	0	98.5%	4.5%
4	98%	0	98.5%	11%
14	98%	0	98.5%	13%

Mayer and Poljakoff-Mayber also point out that factors revealed in the laboratory which affect germination 'may be no more than residual genetic properties which no longer have any direct survival value, and which are retained as long as they have no harmful effect'. Germination at high temperatures in *Juncus squarrosus* may well belong to this category, as it will occur very infrequently in the field, and any wastage will be very small. During the trials a few seedlings germinated when slightly buried (less than 1/8 in. below the surface), possibly due to the rise in surface temperature on bare ground receiving light. If this is so, germination in the dark at high temperatures may be advantageous to the plant, in that more seeds are able to germinate in suitable sites for establishment.

The lower temperature limit to germination will have the effect of preventing germination in the autumn. This is frequently found in autumn-dispersed seeds, and avoids the loss of seedlings during the winter.

SECTION V: ESTABLISHMENT AND GROWTH FORMS

The establishment of the seedlings and the form of mature communities of *Juncus squarrosus* are described in this section. These topics verge on those discussed in sections 2 and 4, but are best dealt with separately.

SEEDLING ESTABLISHMENT

Juncus squarrosus has comparatively slow growth, and several years elapse between germination and the time when an adult plant produces a substantial number of seeds. It has not been possible to follow a seedling through to maturity during the period of study, as the seedlings that germinated during the winter of 1961 - 2 did not produce any inflorescences during the summer of 1963, even when grown in the favourable conditions of the Ecology Greenhouse at the Science Laboratories at Durham. However, these plants in the spring of 1964 are of such a size that they will probably produce a few inflorescences in the summer, judging from observations in the field at Moor House. But it will be at least 1965, their fourth summer of growth, before they reach maturity and produce a substantial number of inflorescences. Under field conditions it is probable that five years will pass between germination and maturity.

After four weeks the seedling has one lateral leaf and an elongated chlorophyllous cotyledon. This now begins to wither,

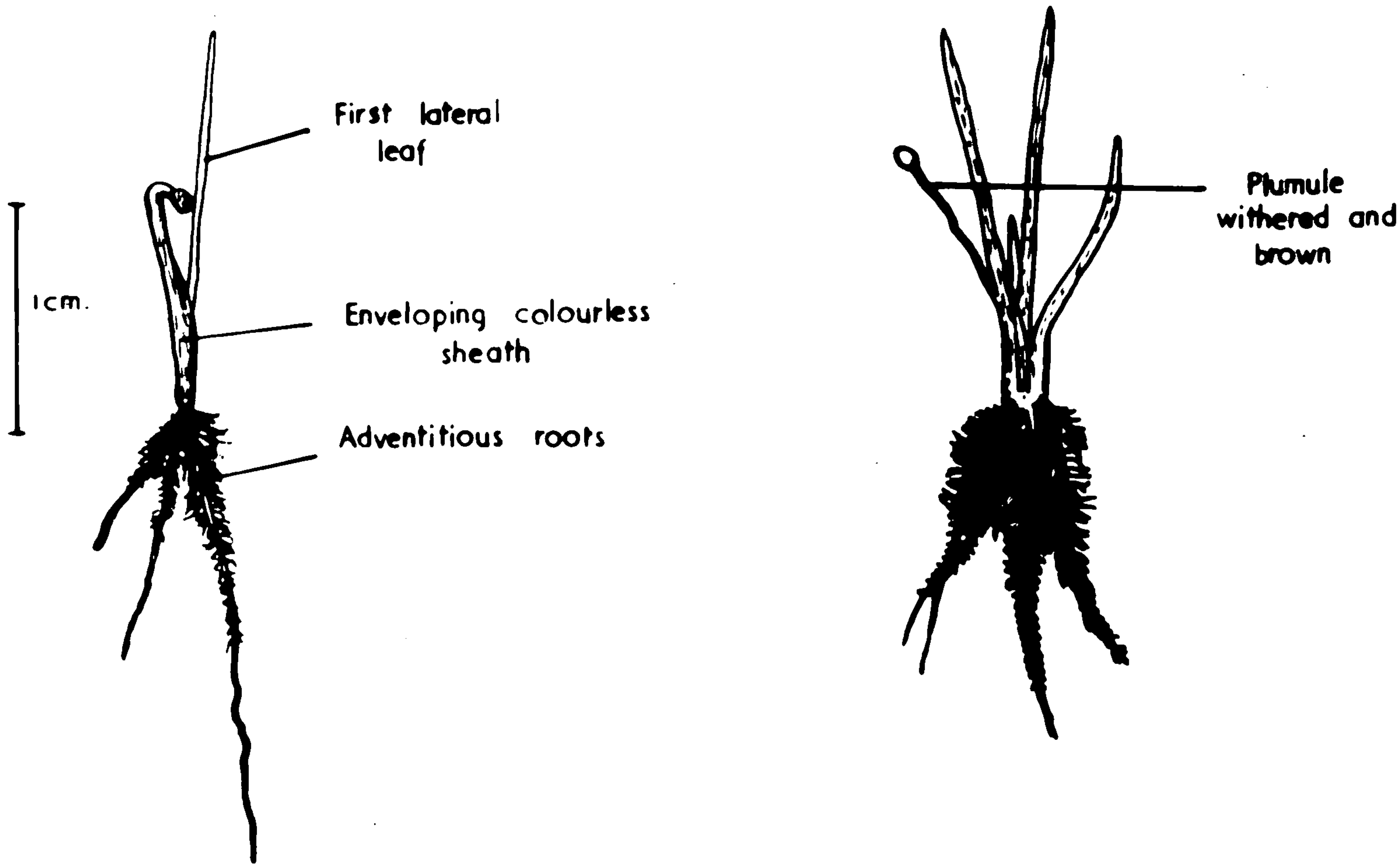


Fig. 5·1. A 4-week old and a 10-week old seedling.

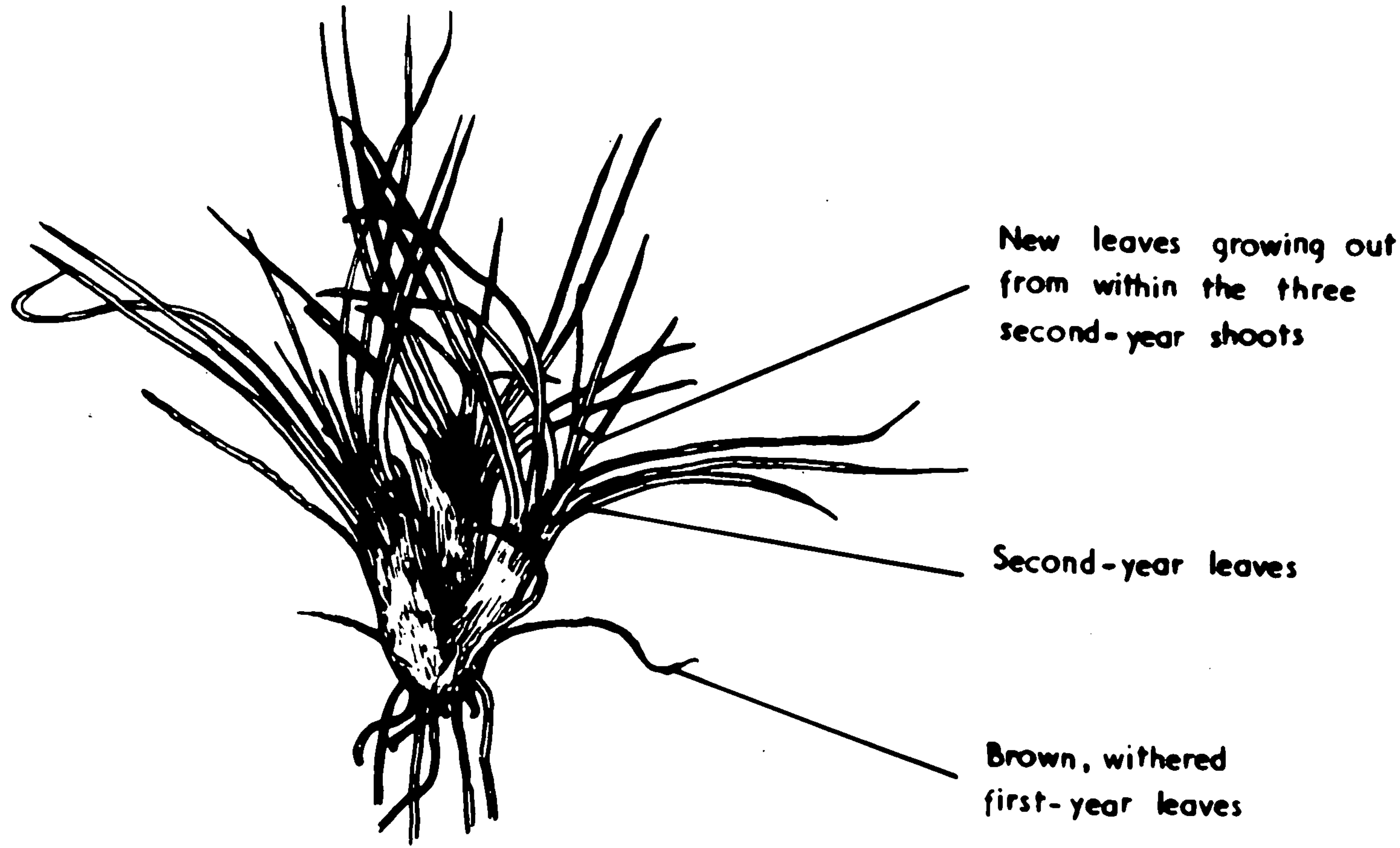


Fig. 5·2. A seedling early in its third year of growth. (Life size) and further lateral leaves are produced (Fig. 5.1). In the greenhouse at Durham and on the windowsill at Moor House the seedlings were about 2 in. (5 cm.) tall and had 8 to 14 leaves at the end of the first growing season.

The leaves produced during the second season are clearly grouped into shoots, usually three in number, but sometimes up to six (Fig. 5.2). The shoots are composed of 6 to 8 leaves which have grown out from inside those of the first season. (Juncus squarrosus is a hemicryptophyte with buds at ground level). By the autumn one plant had 50 leaves, but most had about 25, and the average height was about 3 in. (7 cm.).

It is thought that growth in the third season will be as described in section 2, with all or most of the second season shoots acting as 'front shoots'. Thus each will produce 5 or 6 further shoots, and by the autumn a rosette of Juncus squarrosus will have formed. However it must be emphasised that growth in the field will not occur so rapidly as this.

Factors affecting establishment

It was intended to carry out competition experiments in the field, to show the effect of a sward of Festuca ovina, as compared with no competition, on the germination and establishment of Juncus squarrosus. It is a fact that seedlings of Juncus squarrosus are very rarely found in closed swards, and it was not known whether the explanation was unsuitable germination conditions or a lack of competitive powers in the seedlings. Unfortunately, the experiment was not very successful, because of the difficulties of getting Festuca ovina and Juncus squarrosus to germinate at a particular time, and especially because the seeds of Juncus squarrosus are so light that lateral water movement on the soil surface carried them off or to the margins of the experimental plot. Such lateral water movement is inevitable at Moor House during periods of heavy rain when soils are badly drained.

However, the few seeds of Juncus squarrosus that did germinate were on the plots with no Festuca. After one growing season there was no apparent difference between Juncus squarrosus seedlings planted at the one-year old stage in June into bare plots and into Festuca swards, though these were no more than 1 to 2 in. (2 - 5 cm.) tall. Frost heaving during the winter prevented further observations during the following season, and this must be an important factor affecting seedling establishment in upland areas, probably being most intense on bare unrooted areas.

These tentative results, together with the facts described in section 4, indicate that conditions during germination and the first few days of growth are of primary importance in the establishment of Juncus squarrosus in grazed swards; the amount of competition subsequently imposed on the seedling by a grazed sward is of lesser importance.

The size of mature plants

As mentioned in both the introduction and the section on morphology, the size of _Juncus squarrosus_ varies considerably in response to the environmental conditions. Plants with long leaves (see p. 2.2) also have long inflorescences, and usually have large rosettes with many shoots. An exception to this is when a dense slightly-grazed sward grows up. The leaves grow tall, giving the shoots the form of a vertical cylinder, and thus shading is avoided. The normal well-grown plant in the Moor House area is formed of about 15 living shoots with 120 leaves about 4 in. (10 cm.) long and inflorescences 12 in. (30 cm.) long.

Whilst many of the herbarium specimens in the British Museum, both British and European, were of this size, a considerable number were smaller, more the size of the site G plants (see below), and some were very small. These specimens had many short (2 in. - 5 cm.), thin leaves, and inflorescences only 6 in. (15 cm.) tall and with few florets, and usually came from sandy heaths in southern England, e.g. Wimbledon Common.

When the phytosociological recording was done, the number of rosettes in the quadrats was noted, and related to the estimated cover value, to give some indication of their size. These results are presented in Table 5.1.

Table 5.1. The cover of Juncus squarrosus, and the size and density of the rosettes at the different sites.

	Site (with altitude in feet and soil description)	Average Domin value	Estimated % cover	Rosette Number per 1/4 sq.m.	Rosette Size sq.cm.
G	Cross Fell (2925) felltop podsol	7.7	50	39.1	32
E	House limestone grassland (1850)	4.8	20	15.4	32
A	Knock Fell (2450) peaty podsol	6.7	35	24.8	35
K	Pasture peat (1850)	5.3	25	18.1	35
I	House Hill initial colonisation (1900)	5.4	25	16.7	37
D	Leat bank (1775) gley	5.4	25	15.6	40
F	Dipper (1550) podsol and peaty podsol	5.5	25	14.9	42
B	Trout Beck Foot (1800) alluvial	7.1	45	23.4	48
L	Rough Sike Head (2300) blanket peat	7.9	60	28.2	53
C	Moss Burn alluvial (1850)	6.6	35	13.9	63
H	Teesside green slopes (1800) peaty gley	7.2	45	16.5	68
J	House Hill recolonisation (1900)	7.9	60	21.6	69

As apparent from field observations, the plants of Cross Fell (site G) and the well-drained House limestone grassland (site E) are only half the size of those growing on waterlogged peat at sites H and J. The plants of site I are small, though vigorous, because as yet they are growing in a mound form - the tendency for the rosettes to expand having been met by a bulging upwards. This is usual in the initial stages of colonisation of the mixture of redistributed peat and shattered sandstone boulders left behind after erosion of the blanket bog. Table 5.1 shows that there is no relation between rosette density and rosette size. Both large and small rosettes can occur at low densities (e.g. sites C and E respectively) or high densities (sites L and G), small rosettes at low density having a small cover (20% - E), large rosettes at high density having a high cover (60% - L). Other combinations have intermediate cover values.

Taking the individual quadrats at a site, there was some relation between the number of rosettes present, and the Domin value for the cover of Juncus squarrosus, as shown in Fig. 5.3, but this was not precise, indicating that the rosettes vary in size.

The only standing crop weight given in the literature is 6900 kgm./hectare, with J. effusus being 8000 kgm./hectare (Gorham and Pearsall, 1956), but the type of Juncus squarrosus community is not specified. At Moor House (Rawes and Welch

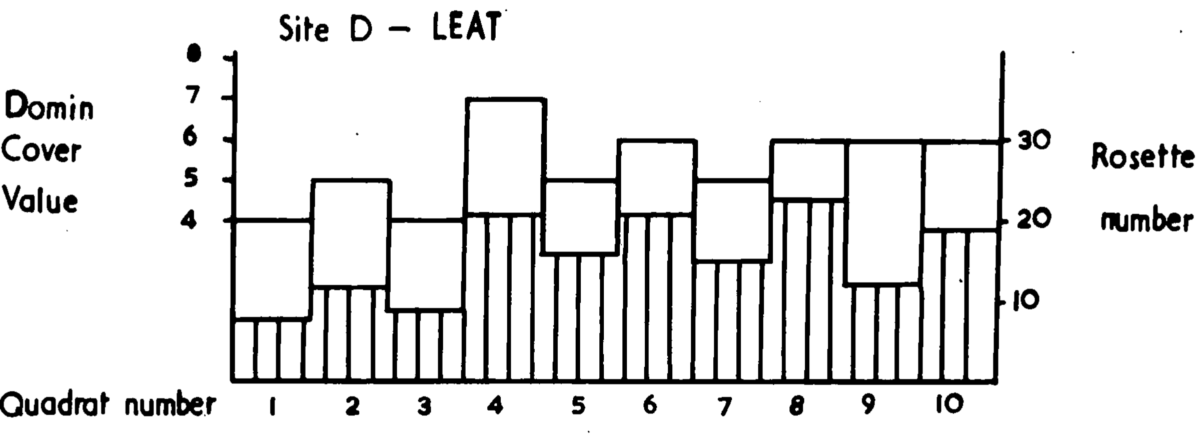


Fig 5·3 The relation of rosette number and Juncus cover in ten quadrats at site D.

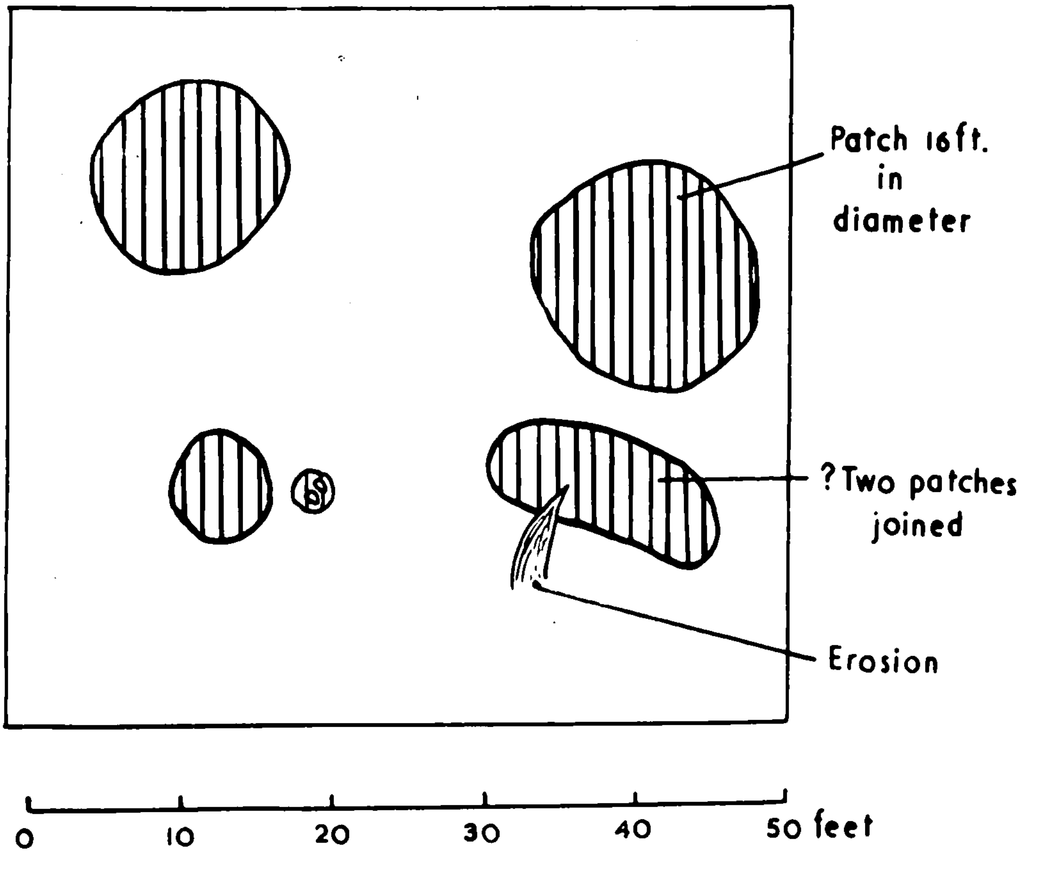


Fig 5·4 Plan of a group of Juncus patches.

unpublished as yet), standing crops of a Juncus squarrosus stand of peaty gley type ranged from 4050 kgm./hectare in spring before growth to a maximum 6150 kgm./hectare. But sorting showed that the actual weights of Juncus squarrosus were 750 and 1300 kgm./hectare respectively.

THE FORM OF JUNCUS SQUARROSUS STANDS

The ability of Juncus squarrosus to spread vegetatively once established, the difficulties of establishment in some swards, and its tolerance of a wide range of conditions, but poor growth in unfavourable habitats are important factors governing the form of stands of Juncus squarrosus.

Three main forms can be distinguished, of which the last is by far the least common:-

1) Fairly uniform stands covering large areas.
2) Heterogenous stands with distinct patches of varying sizes.
3) Groups of scattered plants spread fairly evenly in stands of other species.

The first type is common in the Moor House area, and the stands usually belong to the peaty gley nodum to be described in the next section. Juncus squarrosus is clearly dominant and the plants are large and thriving, being in almost permanently waterlogged conditions. Other species are confined to tussocks in between the rosettes, which under the present grazing regime grow forward each year pushing into the tussocks, whose species then spread on to the decaying leaves left behind in the ageing part of the rosette.

It is very doubtful whether seedlings could become established at the present day in these communities. But vegetative reproduction is quite sufficient to maintain dominance. Most probably the stands have been formed by the coalescing of either very few patches which spread greatly over a long period, or many patches, dating from a time favourable to germination, which spread for a shorter period.

The second type of stand, that of distinct patches, is a transitional type in the formation of either the first or third type. It is to be found colonising swards which are comparatively recent, for example alluvial terraces or stretches of blanket bog in which _Eriophorum vaginatum_ has become the chief species, _Calluna vulgaris_ having declined from various causes.

At the Trout Beck Foot site (B) there are many circular patches of varying diameters up to 4 ft. (1.2 m.), and larger areas which show signs of being derived from 2 or 3 patches. Nearly all show marginal vigour, some being rings with a tall growth of _Festuca ovina_ in the interior, but below which remains of _Juncus squarrosus_ rhizomes can be found.

Inside other patches there are scattered plants of _Juncus squarrosus_, forming a stand similar to that classed as the species-poor gley nodum in the next section. Up to 3 in. (8 cm.) of litter can build up inside a patch, and probably soil changes take place such that the typical sward of Festuca - Agrostis grassland cannot return. Thus it seems that the species-poor gley nodum will result when Juncus squarrosus is able to colonise Festuca - Agrostis grassland on peaty silts.

Examination of the rhizomes gives a growth rate of 2½ in. (6 cm.) in 4 years; this compares with an increment of 0.4 in. (1 cm.) per year for plants on peaty podsols in North Wales (Kershaw and Tallis, 1958). Hence, if the growth rate has been fairly uniform, the majority of patches at the Trout Beck Foot site are no more than 50 years old.

As many patches are present, seedling establishment must have been relatively easy under the grazing regime of recent years. Quite why colonisation did not occur sufficiently long ago for Juncus squarrosus to have spread throughout the suitable area is not known, for this alluvial terrace must be of considerable age.

At many places on the Reserve between 2200 ft. (660 m.) and 2400 ft. (720 m.) there is blanket bog dominated by Eriophorum vaginatum. At Rough Sike Head this slopes at 5 - 10 degrees, and shows signs of sheet erosion in places. Juncus squarrosus patches of different shapes and sizes are present, and the quadrats of site L were positioned on them. A plan of a group of 5 patches of this type at Nether Hearth Sike Head close-by is given to illustrate this (Fig. 5.4).

Marginal vigour is seen in almost all the patches, though the plants throughout are large and well-grown. The litter depth frequently reaches 2½ in. (8 cm.) inside the patches, in contrast to the bare eroding peat or thin cover of _Diplophyllum albicans_ outside. _Festuca ovina_ and some _Deschampsia flexuosa_ grow on the litter, but _Eriophorum vaginatum_ and _Diplophyllum albicans_ are considerably reduced. Certain of the larger patches tend towards the ring type with rather more _Eriophorum_ and less _Juncus_ in the interior, giving a stand typical of the peaty gley nodum, though poor in species. Especially towards the upper margins of the blanket bog, the _Eriophorum_ often passes into _Juncus squarrosus_ communities belonging to this nodum, and these may well be formed from older patches that have coalesced.

Thus it seems that these patch stands are a seral stage in the development of uniform stands belonging to the peaty gley nodum. The patches are most usual where there is a certain amount of flushing down the bog, shown by the presence of _Eriophorum angustifolium_. This is parallelled by the peaty gley stands either being on shallow peat, through which the roots can reach the soil below, or on slightly flushed deeper peat.

In blanket bog communities with good *Sphagnum* growth and little grazing, *Juncus squarrosus* is ousted, but at some time in these areas *Sphagnum* has been reduced and sheet erosion began. *Juncus squarrosus* establishment could then occur. The largest patches at Rough Sike Head are 16 ft. (5 m.) across, and as examination of the rhizomes showed a growth rate of $2\frac{1}{2}$ in. (6 cm.) in 4 years, their approximate age is 160 years.

On the summit of Cross Fell at about 2925 ft. (890 m.) there are 18 patches of *Juncus squarrosus* in one part of the vast plain of *Festuca*-*Deschampsia flexuosa* grassland (site G). Most are circular, with a diameter of about 3 ft. (1 m.), and about half show marginal vigour. Only in some has litter accumulated inside, whilst others have a ring form with a near-normal *Festuca*-*Deschampsia* sward in the centre, and sparse *Juncus squarrosus.* Clearly the habitat is not favourable to *Juncus squarrosus*, probably because of the free drainage and the frost-heaving of the stony soil. The plants are small, as described above, and one dead rosette was found just outside a patch.

Examination of the rhizomes shows that the growth rate is about 1 in. (2 cm.) in 4 years, which would mean that most patches are about 100 years old, whilst the largest patch with a diameter of 6 ft. (1.8 m.) will be considerably older. It would be interesting to know the number of established patches that have become extinct under these adverse conditions, but as competition from other species is never great it is probably few. Assuming this, the very small number of seedlings that have established themselves in a long period over a wide area indicates that conditions are very unsuitable. Light cannot be the controlling factor, as solifluxion provides each year many small areas of bare soil, but probably it also uproots tiny seedlings that germinated during the previous summer.

Growth is so slow under these conditions that it seems the community will persist in the patch state for many years. Drainage is too free and the soil too shallow for Juncus squarrosus to grow large and give rise to stands of the first type, and probably stands of the third type will ultimately result. Already the interior of some rings if of this nature.

The ring distribution pattern has been observed (Penzes, 1960) in quite a few other species, including Juncus subnodulosus, which has an annual increment of 1 inch (2.5 cm.). Penzes distinguishes three types, dependent on the ratio of the growth increment to the stem length. This being small in Juncus squarrosus, it belongs to the fairly dense category.

The ring form of Triglochin maritima in the salt marshes of E. Ireland has been described by Heslop-Harrison and Heslop-Harrison, 1958. The centrifugal growth of the rhizome is much more exact than in Juncus squarrosus, so that no plants remain in the interior of the ring. But the recolonising vegetation is of a different sort to that forming the original sward, coming from a later stage in the halosere. Thus it is argued that the ring phenomenon is not cyclical, but leads to a permanent change in the vegetation. Juncus squarrosus acts similarly, probably by altering the nature of the humus, a change which has been reported also behind advancing fronts of Deschampsia flexuosa in grasslands on shallow limestone soils in Derbyshire (Grime, 1963).

The third type of stand is infrequent in the Moor House area, though the grassy plain on the top of Hard Hill (2250 ft. - 675 m.) is a good example. This was site N in the phyto-sociological analysis.

In the stand there is a tendency for plants of Juncus squarrosus, and Nardus stricta too, to be concentrated in depressions in the hummocky turf, where presumably the water supply is rather better. As on Cross Fell, frost-heaving of the abundant sandstone boulders provides many small areas of bare soil suitable for colonisation by Juncus squarrosus, but it is undecided whether each small group of plants is a result of a single colonisation, or if several groups are the relics of one patch developed from one successful seedling. Evidence presented below from studies in N. Wales points to the latter conclusion, competition from Festuca ovina having been too great for Juncus squarrosus to assume dominance and form a distinct patch.

Pattern in high-level Juncus squarrosus communities on the Carneddau in N. Wales has been described by Kershaw and Tallis, 1958. Festuca ovina and Juncus squarrosus are co-dominant on a peaty pödsol, though their relative proportions vary. The density values given are not comparable to those in Table 5.1, because 'shoots' (see p. 2.2) were counted, but they found the density in a stand of the second type with complete dominance of Juncus squarrosus over Festuca ovina to be nearly twice that in a stand of the third type in which Festuca was more abundant, the H layer thinner and species such as Carex bigelowii, Vaccinium myrtillus, Polytrichum alpinum and Rhacomitrium lanuginosum present.

Both had units of pattern with areas of 200 sq. cm. and 5 sq. m., the first corresponding to rosette size and the second to patch size. But pattern was also detectable at areas of 1600 sq. cm. and 6400 sq. cm. in the stand of the third type, and it is suggested that this is due to competition from Festuca. As conditions in this stand are sub-optimal for Juncus squarrosus, competition tends to restrict the individual plants to areas where conditions are locally more favourable. In contrast in favourable conditions where Juncus squarrosus is completely dominant, occupying 92.7% of the 100 sq. cm. grids in the frame used, the intermediate scales of pattern are eliminated. Two other stands were examined and found to come between the two extremes in grid occupation and scale of pattern.

Kershaw and Tallis are in doubt as to whether the large scale of pattern has been imposed by pre-existing soil heterogeneity, or whether it is the result of vegetative spread from seedlings established for a certain number of years. At Moor House whilst the size of most patches is a function of their age, some especially in limestone grasslands are present on mounds of peat which appear to be relics of blanket bog erosion. Extension off the peat on to the soil will be very slow or impossible, and the present patchy vegetation can be considered as stable, and a result of soil conditions.

SECTION VI: PHYTOSOCIOLOGY

Introduction

It may appear that *Juncus squarrosus* always grows in similar communities, and that it covers most of the ground in any community in which it is present. This is a false impression caused by its conspicuousness. *Juncus squarrosus* seldom covers more than 50% of the ground, and a wide variety of other species accompany it. Often there is more similarity between two communities, one with and the other without *Juncus squarrosus*, than between two *Juncus squarrosus* communities.

With this in mind, it seems that the use of *Juncus squarrosus* as one habitat type by many workers is undesirable. A more accurate description of the *Juncus squarrosus* communities would allow comparisons of similar sites, probably giving more homogeneous results, and would be more meaningful to ecologists concerned with *Juncus squarrosus* elsewhere.

The *Juncus squarrosus* communities at Moor House can be classified to five types, which will be referred to as noda. They can be distinguished simply with a minimum of plant identification, and it is hoped that this classification will be of use to future workers at Moor House.

The noda were established by the method of successive approximation of Poore (1962). It is realised that there is continuous variation between different communities, as is strikingly shown by three ecoclines - Table 6.4, 6.7 and 6.10. But it is convenient to have fixed points on these gradients for reference in describing and comparing plant communities, and these are the noda. Each nodum has its own soil type or types, as Harper (1962) has shown in Lammermuir, and the community clines are normally associated with changing soil type. The noda have been named after the typical soil on which they are found, though on occasions they do occur on other types. The soil nomenclature used in this thesis is that of the Soil Survey of Great Britain in the Kelso and Lauder memoir (1960), and is set out in Appendix 5.

In any single area certain soil types will predominate and the corresponding communities they support will be more frequent than the intermediates. These more frequent communities will be the basis of the noda in that area. Other areas, however, even on the same parent rock, may have slightly different soils because of variations in some climatic factor and there will be corresponding differences in the vegetation. Thus over a large area such as the British Isles, there will be continuous variation in vegetation, and noda have to be chosen arbitrarily.

The past activities of man (sheep-grazing and lead-mining are the most important in this area) cause the phytosociologist extra difficulties in England and Wales, as they have led to the creation of more communities than would be found under natural conditions, or where man's interference has been relatively slight, as in the Scottish Highlands. But all stands, whether thought to be natural or much-changed by man, are described, and the noda determined from their species composition

Following the account of the five noda found in the Moor House area, an attempt is made to relate them to noda established by workers in other parts of Britain. Finally there are descriptions of a few other communities, in which Juncus squarrosus occurs, but which are not found at Moor House.

Methods

During the Autumn of 1961, extensive observations were made on the habitats of Juncus squarrosus. Except for dominant species, e.g. Nardus stricta, Eriophorum vaginatum, other plants were ignored. Sites were selected as characteristic of each habitat type on different soils and at different altitudes, and some were also used in the measurement of reproductive capacity described in section 3. The site locations are shown in Fig. 1.1.

In many places Juncus squarrosus occurs in very marked patches, because of its ability of spreading vegetatively once a seedling has become established. In addition, the soils on which Juncus squarrosus thrives are frequently confined to very limited areas, changing laterally to soils supporting blanket bog or Festuca-Agrostis grassland. Therefore it was decided to use a 50 cm. x 50 cm. quadrat, and to cast it as randomly as possible on to patches of *Juncus squarrosus* or areas in which *Juncus squarrosus* plants were scattered. A metre quadrat would have meant no choice in the placing in many communities, because of the small size of the patches, and would have led to some species from other communities being included in the lists.

At most sites ten quadrats were done, but this was not possible in some places, e.g. flush margins where the *Juncus squarrosus* communities were of very limited extent. On positioning the quadrat, the aspect and slope were noted, and a brief description made of the soil profile alongside. The cover of each species present was assessed on the Domin scale (Appendix 6), and the number of rosettes of *Juncus squarrosus* recorded (this data was presented in the previous section).

Quadratting was started in the middle of June in both 1962 and 1963, and finished by the end of July, except for a few quadrats done at the start of August. The lists of over 200 quadrats were then entered up in a large table. Despite the selection of sites to be representative of one habitat type, more variation was found in some cases between the quadrats of a single site than there was between the sites themselves. The quadrats were grouped into noda, using dominant, constant and faithful species. Finally, since other workers had used larger quadrats, three quadrats of $4m.^2$ were done in a typical community of each nodum, so that comparisons could be made of lists obtained from areas of equal size.

Table 6.1

The species of the Juncus squarrosus noda in the Moor House area. The three columns for each nodum give the Domin scale value for cover in the three large quadrats done as typical of the nodum. Species recorded only in the small quadrats of a nodum are shown thus:- x, constants are underlined.

A = podsol or dry peat nodum, B = peaty gley or wet peat nodum, C = species-poor gley
D = species-rich gley, E = flushed peat nodum.

	A	B	C	D	E
Large quadrat number	123	123	123	123	123
a) throughout					
Festuca ovina	678	353	767	655	542
Juncus squarrosus	765	777	687	655	776
Lophocolea bidentata	222	322	222	322	21

	A	B	C	D	E
b) faithful					
Carex bigelowii	112	x			
Vaccinium myrtillus	222	x			
Cetraria islandica	111	x			
Cladonia impexa	212	x			
C. pyxidata	11				
C. sylvatica	121	x			
Crustaceous rock lichens	11				
Eriophorum vaginatum		5 2			x
Rhytidiadelphus loreus	x	21			
Carex caryophyllea	x			111	
C. ovalis				11	
Juncus effusus				113	x
Poa pratensis				111	
Polygala serpyllifolia				122	
Juncus articulatus					1 1
J. kochii					12
Bellis perennis				x	221
Galium palustris		x			11
Leontodon autumnalis				x	331
Parnassia palustris					1 1
Sagina procumbens					11
Acrocladium cuspidatum				x	444
Bryum pseudotriquetrum					123
Campylium stellatum		x			331
Ctenidium molluscum				x	33
Fissidens osmundoides					333
Cnochophorus virens					11
Philonotis fontana					122
Rhytidiadelphus triquetrus				x	1 1
Aneura pinguis					11
Lophozia quinquedentata					11
Scapania irrigua					332

	A	B	C	D	E
Large quadrat number	123	123	123	123	123
c) differential					
Deschampsia flexuosa	322	555	x		
Galium saxatile	333	1	232	322	
Dicranum scoparium	212	x	11	x	
Hypnum cupressiforme	111	3	322	2	
Plagiothecium undulatum	112	2	x		
Pleurozium schreberi	435	x	321	2	
Polytrichum commune	344	455	x		
Rhytidiadelphus squarrosus	222	222	333	544	x
Calypogeia trichomanis	x	112	+11		
Lophozia floerkii	232	221	11	1	
Ptilidium ciliare	333	332	x	12	
Cladonia furcata	121	x	1		
Agrostis tenuis	2	x	433	444	1
Anthoxanthum odoratum		x	332	222	233
Carex nigra	x	233	x	311	225
Deschampsia cespitosa			2	x	312
Eriophorum angustifolium		1			1
Luzula campestris	x	11	323	323	111
Nardus stricta	231	452	332	566	464
Potentilla erecta	x	1	x	343	231
Aulacomnium palustre		443		222	
Hylocomium splendens	1		322	443	1+
Mnium hornum	x	x	21		112
Carex demissa				1	1 2
C. flacca				11	312
C. panicea				21	2
C. pulicaris				233	321
Festuca rubra				1 1	433
Holcus lanatus				32	111
Cardamine pratensis			x	121	123
Cerastium holosteoides			x	112	21
Cirsium palustre				221	11
Epilobium anagallidifolium				1	+22
Equisetum palustre				112	112
Euphrasia sp.	x			11	12
Prunella vulgaris				121	33
Ranunculus acris				122	2
R. flammula				1	12
Selaginella selaginoides				2	222
Taraxacum officinale				111	1
Trifolium repens				4 3	223
Viola riviniana				221	22
Mnium punctatum				111	243
M. undulatum				222	123
Thuidium tamariscinum				112	2
Leptoscyphus taylori			x	1	111

The nomenclature for the species in the following tables is given in Appendix 6, whilst Appendix 7 gives site locations and soil data.is in Appendix 8.

The Juncus squarrosus communities of the Moor House area.

The salient features which differentiate the five noda are shown in Table 6.1. It is clear that two noda, the species-rich gley and the flushed peat, contain many more species than the others, and share a considerable group of base-demanding species. But each has many characteristic species (i.e. confined to, or more widespread in it), which must be more sensitive to whether the immediate sub-stratum is a soil or a peat. Equivalent to these two noda, but containing many fewer species are respectively the species-poor gley nodum and the peaty gley nodum.

Lastly, on drier soils there is the podsol nodum, which is not always very sharply distinguished from the last two. Communities on peaty podsols are intermediate between it and the peaty gley nodum, but usually belong to the podsol, as they lack certain species, e.g. Carex nigra, Eriophorum vaginatum, Aulacomnium palustre and Calypogeia trichomanis which demand permanently waterlogged conditions.

The podsol and peaty gley have in common several plants characteristic of raw humus, including Deschampsia flexuosa, Polytrichum commune, Lophozia floerkii and Ptilidium ciliare which are much less abundant in the other noda. In turn, species such as Agrostis tenuis, Anthoxanthum odoratum, Luzula campestris and Hylocomium splendens are infrequent in the podsolic noda, but have considerable cover value in the species-poor and species-rich gley noda.

Festuca ovina and Lophocolea bidentata occur with Juncus squarrosus in all its Moor House habitats. Lophocolea has an especially close relation, as it is almost always present in the ground layer around a Juncus rosette, growing on the decayed leaves and obtaining its light from the inverted cone coming down into the sward because of the spreading of the rosette leaves.

The peaty gley nodum is the most widespread in the Moor House region, and corresponds with the Juncètum squarrosi sub-alpinum shown by Eddy (unpublished) on his vegetation map of the Moor House N.N.R. This community is obviously dominated by Juncus squarrosus, whereas in the others dominance is shared or Juncus squarrosus is only a community member, and therefore they are sometimes named after the other dominant species. The flushed-peat nodum is the least extensive, being a marginal community around calcareous springs and flushes, which are usually so small that their vegetation zones have to be mapped as one in large-scale vegetation surveying. The relations of my other noda with Eddy's mapping units will be discussed when the noda are dealt with one by one below.

The podsol nodum (Table 6.2)

45 quadrats from seven different sites have been joined to form the podsol nodum. 50 species occur, but 36 of these are lower plants. Lichens are plentiful in the fell-top podsol lists, but are almost absent in the lower and peaty podsols. Except for the lichens, there are fewer species in the climatically extreme conditions near the summit of Cross Fell. _Galium saxatile_, _Hypnum cupressiforme_, _Plagiothecium undulatum_, _Polytrichum commune_, _Rhytidiadelphus squarrosus_ show a reduced frequency or are absent in these 10 quadrats, which have been omitted from the calculations determining the constant species of the nodum.

Besides _Festuca ovina_ and _Lophocolea bidentata_, there are 7 constant species (in 80% or more of lists) and 3 near-constant species (in 50-80% of lists). _Deschampsia flexuosa_, _Polytrichum commune_ and _Ptilidium ciliare_ are constants shared with the peaty gley nodum, though in this _Polytrichum_ has more cover, and _Galium saxatile_ and _Rhytidiadelphus squarrosus_ are shared with the species-poor gley nodum. _Pleurozium schreberi_ and _Lophozia floerkii_ are the only characteristic constants of the nodum, and occur in others though with reduced frequency and cover. Of the near-constants, _Vaccinium myrtillus_ is characteristic, but _Agrostis tenuis_ and _Hypnum cupressiforme_ are more frequent in the species-poor gley nodum. Thus the

PODSOL NODUM

Table 6.2

$4\ m^2$ quadrats I — $\frac{1}{4}\ m^2$ quadrats - - - -

Site (height in feet)	Hard Hill 2250			Hard Hill 2250										Dipper 1500		Knock Fell 2450										Pasture 1850	W.side Knock 1850						Knock Fell 2500						Cross Fell 2925									
Soil	felltop podsol			felltop podsol										iron podsol on whinsill		truncated-peat podsol over calcareous drift										podsol	peaty podsol over scree						peaty podsol						felltop podsol									
Quadrat Number	1	2	3	N1	N2	N3	N4	N5	N6	N7	N8	N9	Nx	F5	F6	A1	A2	A3	A4	A5	A6	A7	A8	A9	Ax	Ex	T1	T2	T3	T4	T5	T6	P1	P2	P3	P4	P5	P6	G1	G2	G3	G4	G5	G6	G7	G8	G9	Gx
Aspect					W	SW		SE						E	NE	SW		NE		NE	W	W	NW	N		NW	NW	W	NW	N	NW		N	N	N	W			SW	SW						W	W	W
Slope					2	1		2						3	5	1		4		2	1	2	1	2		5	2	2	3	2	2		1	1	1	1			1	1						2	1	1
Agrostis canina		2																	1																	1		1										
A. tenuis			2						1	1	2					2	2	2	3	3	2	1	2	1	2					1			1	1	1	2	1	1										
Carex bigelowii	1	1	2					1	1		1	1															1			1			2				1			2	1	1		1	1			
C. caryophyllea																				1																												
C. nigra																											1	2	2	2		2																
Deschampsia flexuosa	3	2	2	2	2	3	1	2	2	2	1	3	1	1	1	2	2	1	3	2	1	3	2	1	1	3	4	4	5	2	5	3	5	6	5	4	5	7	3	1	2	2	3	2	3	3	2	3
Festuca ovina	6	7	8	7	8	7	8	7	7	8	7	7	7	6	5	7	6	7	6	6	6	7	7	6	7	6	6	6	6	7	6	5	5	4	4	5	6	4	7	7	6	5	7	6	5	4	7	6
Juncus squarrosus	7	6	5	7	6	7	5	6	6	6	7	6	6	5	6	7	7	6	6	5	7	7	7	8	7	5	6	7	7	6	8	6	7	7	8	8	7	7	8	7	8	8	7	8	8	8	7	8
Luzula campestris														1	1	1										1																						
Molinia caerulea														4	2																																	
Nardus stricta	2	3	1					2	3			4		7	6					3						5			2	3	2	1																
Euphrasia sp.														2																																		
Galium saxatile	3	3	3	2	2	2	3	2	2	2	1	1	2	3	3	3	2	3	2	3	2	2	2	2	3	1		2	1	4	2	2	2	1	2	3	3	1	1								x	1
Potentilla erecta														1	3	2																																
Vaccinium myrtillus	2	2	2	2	1	1	1	1			2	1	1					2	1	2		1		2			1		3		1	2	2	1	1	1	1	1	1	2			2	3	1		2	1
V. vitis-idaea			1																																													
Dicranum fuscescens																																								1			1	1		1		
D. scoparium	2	1	2	1	1			1		1	1		1	3		1		2										1	1			1							2	2	1			1	1	2	1	1
Hylocomium splendens	1													1	1			1								2																						
Hypnum cupressiforme	1	1	1	2	2	2	2	2	3	2	1	1	1	3	2	2	2	2	1	1	2	1				1		1	1		1	2	2															
Mnium hornum																				1						3																						
M. longirostrum																										3																						
Plagiothecium undulatum	1	1	2	1			1			1	1	1	2						2	2	1		3		2		2							1		4	2	4										
Pleurozium schreberi	4	3	5	2	1	2	2	3	1	1	2	2	2	3	3	1	2	1	1	1	2		1	1	1	2	4	4	4	3	3	3	3	2	3		2				1	1	2		2		2	2
Pohlia nutans																																														1		
Polytrichum alpestre	1																																															
P. alpinum			1																															1			2											
P. commune	3	4	4	2	2	3	2	2	3	2	2	2	2	x	3	4	5	4	4	4	3	3	3	4	4	2	3	2	2	2	2	3	4	3	3	2	3	2	2		3	3		1	2		4	2
Rhacomitrium lanuginosum																																								1		1				1		
Rhytidiadelphus loreus																											2		1									2										
R. squarrosus	2	2	2	2	1	1	2		1		1	2	1	2	2	2	1	1	1	2	3	3	2	2	2	2	2	3	2	2	3	3	3	3	3	3	2	1			1		2		1		2	3
Splachnum ovatum	1																															1						1				1			1			
Calypogeia trichomanis															1				1												1																	
Lepidozia reptans																									1																							
Lophocolea bidentata	2	2	2	2	1	1			1	2	1	1	2	3	2	2	3	2	1	2	2	2	1	1	1	1	2	2	1	1	2		2	3	3	1	1											
Lophozia floerkii	2	3	2		1	2	1	1	1	1	1	1	1	1	1	2	2	3	1	1				2	2	21	1	2			1	1		1	1		2	2	3	3	3	3	3	2	2	3	2	2
L. lycopodioides																1	1	1							1								1		1													
L. ventricosa			1	1	1														1		x	1		3	2			1					2	2	2		2									1		
Ptilidium ciliare	3	3	3	2	2	2	2	2	2	2	2	2	1		1	1	2	2		2		1					1	1	2	2	1	2	2		1	1	1	2	2	1	2	2	3	2	3	1	2	2
Cetraria aculeata	1									1																													2	2	1	2	2	1	1	1	1	1
C. islandica	1	1	1	1	1	1	1	1	1				1								1																		3	2	2	2	3	2	2	3	2	1
Cladonia floerkeana																																														1		
C. furcata	1	2	1	1	1	1	1	1	1	1	1	1	1																										1		1	1	1	1		1		1
C. impexa	2	1	2	1	1	1			1				1																																			
C. papillaria		1																																														
C. pyxidata	1	1							1																																					1		
C. squamosa						1																																										
C. sylvatica	1	2	1	1	1	1	1	1	1	2		1																											1	2	1	1	1	1		1	1	1
C. uncialis			1																																													
Crustaceous rock lichen		1	1			1																																										

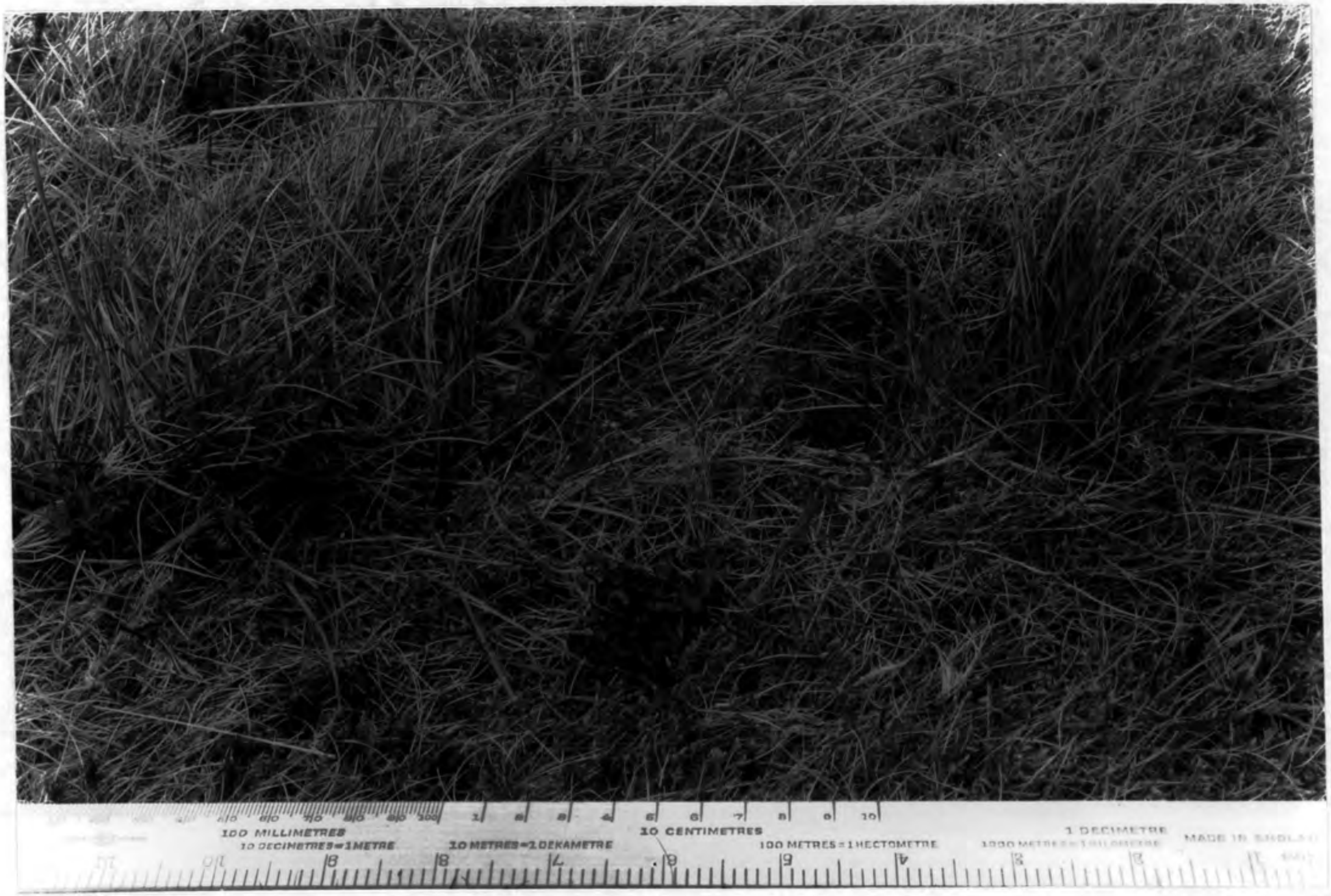


Plate 4 - Section 6: Close-up of a sward belonging to the podsol nodum on Hard Hill. (Note the Pleurozium scherberi and Cetraria islandica in the foreground).

podsol nodum is recognised by the grouping of constants, rather than by characteristic ones. Apart from the lichens, which are confined to one facies, there are no characteristic species.

Stands of the nodum (Plate 4) are typically fairly grassy, Festuca ovina having a greater cover than Juncus squarrosus in most lists, and the Juncus squarrosus plants themselves are smaller than in wetter habitats. The podsol community grades into a Festucetum, with frequent Deschampsia flexuosa, whilst at the other extreme the peaty podsol community grades into Juncetum squarrosi sub-alpinum (as shown in Table 6.4) with Potentilla erecta and Polytrichum commune more abundant, and Carex nigra, Aulacomnium palustre and Calypogeia trichomanis present. Eddy has not mapped this nodum as a separate unit, as frequently there is a complex of intermediates between the two extreme associations, but assigns its stands to one or other, or to Nardetum, according to the relative abundance of these three species.

In some stands, Juncus squarrosus communities form isolated ring patches in a Festuca sward (e.g. the G quadrats on Cross Fell were done in such patches), while in other places groups of Juncus squarrosus and Nardus stricta plants are scattered in Festuca swards (the third type of stand described in the last section). Where they become more numerous, the vegetation can be assigned to the podsol nodum. It is sometimes said that such Juncus squarrosus communities develop when species-

Table 6.3

PEATY GLEY NODUM

Sites:

- 4m² quadrats (1–3): Teesside green slopes below blanket bog 1800'
- ¼m² quadrats (P6–Px): Knock Fell 2500'
- H1–H8: Teesside green slopes on Silo Hill and Spur Hill (7 and 8) 1800'
- S1–Sx: West side of Knock Fell at 1750'. A wet shelf at foot of a slope with sandstone scree below
- J1–Jx: House Hill recolonisation complex on wet spreads of redistributed peat among eroding blanket peat mounds 1900'
- O1–Ox: Bog End Trackway (slightly flushed blanket bog used as track in mining days, and recolonised by Js) - 1850'
- K1–K7: Moor House Pasture blanket bog - 1850'
- K8–16: formerly winter-grazed, excluding Calluna and then colonised by J.squarrosus
- U1–Ux: S.W. slope of Bellbeaver Rigg, close to Lady Vein, winter-grazed peaty gley 1800'
- F8–Fx: Dipper 1550'

Quadrat Number	1	2	3	P6	P7	P8	Px	H1	H2	H3	H4	H5	H6	H7	H8
Slope	4	4	2	-	-	-	1	5	5	5	8	5	1	3	4
Aspect	W	SE	SE				NE	S	S	S	E	E	SE	SE	SE
Depth of H horizon	60	30	35	20	30	25	30	35	30	40	25	25	50	50	50
Agrostis canina											2			1	
A.stolonifera															
A.tenuis									1		2				
Anthoxanthum odoratum															
Carex bigelowii				1	3	1	1								
C.curta															
C.echinata	1														
C.nigra	2	3	3					2	2	2	2		3	3	
Deschampsia flexuosa	5	5	5	5	5	6	5	1	1	x		2	1		1
Eriophorum angustifolium	1							1	x		1		2		1
E.vaginatum	5		2				3	5	4	4				4	
Festuca ovina	3	5	3	5	5	4	5	4	6	5	4	5	5	5	5
Juncus effusus										2					
J.squarrosus	7	7	7	8	7	7	7	7	7	8	8	8	7	6	7
Luzula campestris		1	1					1						1	
Nardus stricta	4	5	2							4					1
Calluna vulgaris												x			
Empetrum nigrum															
Galium palustre															
G.saxatile	1					1			1	1	1			4	
Potentilla erecta	1										1		x	1	
Vaccinium myrtillus						1									
Acrocladium stramineum															
Aulacomnium palustre	4	4	3					2	1		1	x			2
Campylium stellatum															
Dicranum scoparium								2							
Drepanocladus fluitans															
Hypnum cupressiforme	3					2								x	
Mnium hornum															
Plagiothecium undulatum	2					2				3	3		2		
Pleurozium schreberi															
Pohlia nutans															
Polytrichum alpinum					1										
P.commune	4	5	5	3	3	4	2	3	3	3	4	4	4	5	4
Rhytidiadelphus loreus		2	1												
R.squarrosus	2	2	2	2	1	1				2				1	1
Sphagnum cuspidatum	x														
S.palustre															
S.recurvum											5		5	4	
S.plumulosum															
S.subsecundum															
Splachnum ovatum	1								x						
Calypogeia trichomanis	1	1	2	2		2	1	2	2	1	2	1	2	1	
Cephalozia bicuspidata															
Diplophyllum albicans				1											
Lepidozia reptans															
Leptoscyphus anomala															
Lophocolea bidentata	3	2	2			2		2	3		1	2	x	x	2
Lophozia floerkii	2	2	1	2	2	2									
L.lycopodioides				1	1										
L.ventricosa				1	1	1				x	1				
Ptilidium ciliare	3	3	2	2	4	3	2	1		1		1		1	
Cetraria islandica				1											
Cladonia furcata							1								
C.impexa							1								
C.sylvatica															

Quadrat Number	S1	S2	S3	S4	S5	S6	S7	S8	S9	Sx	J1	J2	J3	J4	J5	J6	J7	J8	J9	Jx
Slope	1	1	1	1	2	3	1	2	2	2	-	-	2	1	2	2	-	-	-	2
Aspect	W	W	NW	NW	NW	NW	NW	W	N	N			S	SW	E	S				N
Depth of H horizon	10	30	20	15	20	30	20	15	15	25	4	10	30	40	40	10	7	50	15	8
Agrostis canina				1	1			1							2					
A.stolonifera							1													
A.tenuis																				
Anthoxanthum odoratum																				
Carex bigelowii																				
C.curta																		2		
C.echinata																				
C.nigra	1	1	2		1	1			1	2				4				1	1	
Deschampsia flexuosa	5	4	4	5	4	4	3	4	4	5					1					1
Eriophorum angustifolium												2	4	2				3		2
E.vaginatum																				4
Festuca ovina			2	3	3	4	4	2	4	5	3	3	1	2	6	5	4		5	5
Juncus effusus																				
J.squarrosus	8	8	8	8	7	8	8	8	8	7	9	8	7	8	7	8	8	8	8	8
Luzula campestris																				
Nardus stricta			1	1		1		1					3							x
Calluna vulgaris												1								
Empetrum nigrum												1								
Galium palustre																				
G.saxatile						1	1	1							1					
Potentilla erecta	1		1	1	1	1	1	2		1						1				
Vaccinium myrtillus	2	1	2			2	1	1	2	1										
Acrocladium stramineum														x		x	3			
Aulacomnium palustre																				
Campylium stellatum																				
Dicranum scoparium	1	1	2			2			2	1		2								1
Drepanocladus fluitans														1						
Hypnum cupressiforme	2	1	2	2	1	2	2	1										x		2
Mnium hornum																				
Plagiothecium undulatum							2	1	3	2									3	
Pleurozium schreberi			1			2	1	1	1	1		1				4			1	
Pohlia nutans																	x			
Polytrichum alpinum																				
P.commune	4	5	4	5	5	5	5	5	5	4	8		6	6	4	8	5		5	1
Rhytidiadelphus loreus	1	1	2	2	1	2	2	2	3	2									2	1
R.squarrosus					1	1		1		1										x
Sphagnum cuspidatum	2	1						2												
S.palustre												4				2				1
S.recurvum					3		2	1						2	5	7	7			4
S.plumulosum																			2	
S.subsecundum																				
Splachnum ovatum										1					x					
Calypogeia trichomanis		2	1	2	1	1	1	1		1	8	2	2	2	2	3	1	2	3	2
Cephalozia bicuspidata											1									
Diplophyllum albicans	3	1					2	2												
Lepidozia reptans									1											
Leptoscyphus anomala																x			x	
Lophocolea bidentata		3	2	1		2	2	2	2	2	4	3	x	1	2	1	1		3	
Lophozia floerkii		1	1			2	2	3			2	4							2	1
L.lycopodioides																				
L.ventricosa						1	1	2			4	2			2	1	1		1	x
Ptilidium ciliare	1	1	1	2		1			1		3	3			3			4	3	4
Cetraria islandica																				
Cladonia furcata																				
C.impexa																				
C.sylvatica						1														

Quadrat Number	O1	O2	O3	O4	O5	O6	O7	O8	O9	Ox	K1	K2	K3	K4	K5	K6	K7
Slope	2	2	1	2	1	1	-	-	2	2	4	3	3	1	1	2	1
Aspect	SE	SE	SE	S	S	S			SE	SE	SW	SW	SW	S	S	SW	SW
Depth of H horizon	40	40	30	40	80	90	100	50	80	100	70	100	80	40	35	40	120
Agrostis canina																	
A.stolonifera																	
A.tenuis														1			
Anthoxanthum odoratum																	
Carex bigelowii																	
C.curta																	
C.echinata																	
C.nigra	3	3	4		4		3	3	3	2				2	3	3	
Deschampsia flexuosa	4	4	2	4	2	3	4	4	4	3	6	4	6	6	3	4	5
Eriophorum angustifolium	2	2	1	2	1	2	2		2	1			2	1		2	
E.vaginatum			x	3		5	1			3	4	3					6
Festuca ovina	3	4	3	3	5	3	5	2	4	2	5	6	6	2	4	6	5
Juncus effusus																	
J.squarrosus	6	7	8	7	7	6	6	8	7	8	5	5	4	5	8	5	5
Luzula campestris																	
Nardus stricta												2		1			
Calluna vulgaris																	
Empetrum nigrum																	
Galium palustre																	
G.saxatile													1			x	
Potentilla erecta			1					1									
Vaccinium myrtillus																	
Acrocladium stramineum																	
Aulacomnium palustre	2	3	2	2	1	4	3	3		1		1	1				1
Campylium stellatum																	
Dicranum scoparium												2					
Drepanocladus fluitans																	
Hypnum cupressiforme																	
Mnium hornum																	
Plagiothecium undulatum	1			1		1	1	3			3	3	3	1	2	2	2
Pleurozium schreberi	1														1	1	1
Pohlia nutans																	
Polytrichum alpinum																	
P.commune	5	4	4	4	1	4	4	2	2	2	3	1	1	2	1	1	
Rhytidiadelphus loreus	1	1		1		2					1	1	1				
R.squarrosus				1			4	1									
Sphagnum cuspidatum																	
S.palustre																	
S.recurvum																	
S.plumulosum																	
S.subsecundum																	
Splachnum ovatum																	
Calypogeia trichomanis	2	1	1	2	1	2		1	1		1	1	2	2			2
Cephalozia bicuspidata																	1
Diplophyllum albicans																	
Lepidozia reptans																	
Leptoscyphus anomala						1											
Lophocolea bidentata	2	2	2	2	1	2	1	2	3	2		1		2			
Lophozia floerkii					1							3	1	3		1	1
L.lycopodioides																	
L.ventricosa																	
Ptilidium ciliare	3	4	5	4	4	3	3		2	3			1	3		1	2
Cetraria islandica	1																
Cladonia furcata																	
C.impexa																	
C.sylvatica																	

Quadrat Number	K8	K9	Kx	11	12	13	14	15	16	U1	U2	U3	U4	U5	U6	U7	U8	U9	Ux	F8	F9	Fx
Slope	1	1	2	2	2	2	2	2	2	1	1	1	1	1	2	1	1	1	1	5	2	3
Aspect	SW	SW	SW	SW	SW	SW	SW	SW	SW	W	W	W	W	W	W	SW	NW	W	W	E	E	NE
Depth of H horizon	100	50	70	100	100	80	80	45	100	40	40	50	35	50	40	35	30	50	35	5	5	5
Agrostis canina				2	3					1	2	2	2	1	1	2	2	2	2			
A.stolonifera						1															1	1
A.tenuis						3	3	2	2					1			1					1
Anthoxanthum odoratum																						1
Carex bigelowii																						
C.curta																						
C.echinata																						
C.nigra	3			5	3	1	1	1	1				2				2			3	4	3
Deschampsia flexuosa	3	5	6	3	1	1				2	3	2	2	3	2	2	3	3	3			
Eriophorum angustifolium				3	3	1	2	3	3													
E.vaginatum	4	1	2			2																
Festuca ovina	7	6	5	5	6	5	6	6	5	5	6	6	5	5	5	7	6	6	5	2		2
Juncus effusus																						
J.squarrosus	4	6	5	5	6	6	6	4	7	8	7	8	8	8	7	7	8	7	8	5	7	6
Luzula campestris						1	1					1							1	2		1
Nardus stricta	1	1			4						2			2	1				1	6	2	1
Calluna vulgaris																						
Empetrum nigrum																						
Galium palustre																				1		
G.saxatile						1	3			1		2	x	1	1	1		2	2			
Potentilla erecta																			1	3	2	1
Vaccinium myrtillus													1									
Acrocladium stramineum						x		x												2		1
Aulacomnium palustre		1	1	1		2	1	1		1	1	2	1	2	3	1	2	3				
Campylium stellatum																				1	1	
Dicranum scoparium										1								1				
Drepanocladus fluitans	1																			1		
Hypnum cupressiforme										1						1		2	2	1		x
Mnium hornum																				1		
Plagiothecium undulatum	1	2	1		1	3	1	x		2	3	4	1	1		3		1	1			
Pleurozium schreberi	1									2	1	1	1	2	2	1	2	1				1
Pohlia nutans														1								1
Polytrichum alpinum																						
P.commune	1			3	4	1		5	3	3	3	3	3	3	3	3	4	2	3	4	5	6
Rhytidiadelphus loreus				1	2	2	2	1					1	1	2	1		1				
R.squarrosus										3	2	2	2	1	1	2	2	1	3	2		1
Sphagnum cuspidatum																						
S.palustre																						
S.recurvum																						
S.plumulosum																	2	1				
S.subsecundum																				2	1	1
Splachnum ovatum										1												1
Calypogeia trichomanis	1	1	1	3	3	1		2	2	1	1		1	1	1	1	2	1				3
Cephalozia bicuspidata	3			1		x	x															
Diplophyllum albicans																						
Lepidozia reptans																						
Leptoscyphus anomala																						
Lophocolea bidentata		1		1		3	3	x	2	2	1	2	2	2	2	2	2	3	3			2
Lophozia floerkii			2					x		1	1					1		1	1			
L.lycopodioides																						
L.ventricosa			1	2	2			x														
Ptilidium ciliare			1							1	2	1	2	1	1	1	1	1				
Cetraria islandica																						
Cladonia furcata																						
C.impexa																						
C.sylvatica																						

poor Agrosto-Festucetum is over-grazed, but these relationships will be discussed later.

Over the Reserve as a whole, the nodum has considerable extent, but is chiefly confined to the western escarpment and the summit ridge.

The peaty gley nodum (Table 6.3)

71 quadrats from 8 different sites belong to the nodum, but contain only 56 species, in contrast to the 96 species occurring in the 12 quadrats in the flushed-peat nodum. Juncus squarrosus is the clear dominant, and Polytrichum commune frequently has a high cover-value. Between the Juncus rosettes there are clumps containing Festuca ovina, Deschampsia flexuosa and Carex nigra, but herbs are scarce in the dense growth. Lichens are very infrequent in the lists, but bryophytes are plentiful in most.

There are only three constants, of which Calypogeia trichomanis is characteristic, and Polytrichum commune more abundant here than elsewhere. The other, Festuca ovina, and Lophocolea bidentata, a near-constant, are less abundant than in the podsol nodum, and Deschampsia flexuosa and Ptilidium ciliare are only near-constants, but have high cover-values in some stands. The other near-constants are Plagiothecium undulatum, characteristic of the nodum, and Carex nigra, which is a constant of the flushed-peat nodum. There are several

Table 6.4.

The gradient from peaty podsol to peaty gley to blanket bog.

Soil	PEATY PODSOL			PEATY GLEY			BLANKET BOG
Site	Knock Fell 2450'	W.side of Knock 1850'	Knock Fell 2500'	Knock Fell 2500'	West side of Knock 1750'	Teesside green slopes 1750'	Teesside green slopes 1750'
Soil	truncated-peat podsol	peaty podsol over scree	peaty podsol	peaty gley	peaty gley over sandstone scree	peaty gley and slightly flushed blanket peat	blanket bog (margin of green slope)
Quadrat numbers	A1–A9, Ax	T1–T6	P1–P5, P9	P6, P7, P8, Px	S1–S9, Sx	H1–H8	W1–W9

Quadrat number	A1	A2	A3	A4	A5	A6	A7	A8	A9	Ax	T1	T2	T3	T4	T5	T6
A) OVERALL																
Agrostis canina				1												
A.stolonifera																
Deschampsia flexuosa	2	2	1	3	2	1	3	2	1	1	4	4	5	2	5	3
Festuca ovina	7	6	7	6	6	6	7	7	6	7	6	6	6	7	6	5
Juncus effusus																
J.squarrosus	7	7	6	6	5	7	7	7	8	7	6	7	7	6	8	6
Luzula campestris	1															
Nardus stricta					3								2	3	2	1
Dicranum scoparium	1		2									1	1			1
Plagiothecium undulatum				2	2	1		3		2	2					
Pleurozium schreberi	1	2	1	1	1	2		1	1	1	4	4	4	3	3	3
Polytrichum alpinum																
P.commune	4	5	4	4	4	3	3	3	4	4	3	2	2	2	2	3
Splachnum ovatum																1
Lepidozia reptans										1						
Lophocolea bidentata	2	3	2	1	2	2	2	1	1	1	2	2	1	1	2	
Lophozia ventricosa				1		x	1		3	2		1				
Ptilidium ciliare	1	2	2		2		1				1	1	2	2	1	2
Cladonia furcata																
C.impexa																
C.sylvatica																
B) PODSOL-FAVOURING																
Agrostis tenuis	2	2	2	3	3	2	1	2	1	2				1		
Carex bigelowii											1			1		
C.caryophyllea					1											
Galium saxatile	3	2	3	2	3	2	2	2	2	3		2	1	4	2	2
Vaccinium myrtillus			2	1	2		1		2		1		3		1	2
Hypnum cupressiforme	2	2	2	1	1	2	1					1	1		1	2
Hylocomium splendens			1													
Mnium hornum					1											
Rhytidiadelphus squarr.	2	1	1	1	2	3	3	2	2	2	2	3	2	3	3	3
Lophozia floerkii	2	2	3	1	1				2	2	1	2			1	1
L.lycopodioides	1	1	1							1						
Cetraria islandica						1										
C) PEATY-GLEY FAVOURING																
Carex nigra											1	2	2	2		2
Potentilla erecta	2															
Rhytidiadelphus loreus											2		1			
Sphagnum cuspidatum																
S.recurvum																
Calypogeia trichomanis				1											1	
Diplophyllum albicans																
D) BLANKET-BOG FAVOURING																
Eriophorum angustifolium																
E.vaginatum																
Calluna vulgaris																
Empetrum nigrum																
Aulacomnium palustre																
Sphagnum plumulosum																

Quadrat number	P1	P2	P3	P4	P5	P9	P6	P7	P8	Px
A) OVERALL										
Agrostis canina				1		1				
A.stolonifera										
Deschampsia flexuosa	5	6	5	4	5	7	5	5	6	5
Festuca ovina	5	4	4	5	6	4	5	5	4	5
Juncus effusus										
J.squarrosus	7	7	8	8	7	7	8	7	7	7
Luzula campestris										
Nardus stricta										
Dicranum scoparium										
Plagiothecium undulatum		1		4	2	4			2	
Pleurozium schreberi	3	2	3		2					
Polytrichum alpinum		1			2					
P.commune	4	3	3	2	3	2	3	3	4	2
Splachnum ovatum						1				
Lepidozia reptans										
Lophocolea bidentata	2	3	3	1	1				2	
Lophozia ventricosa	2	2	2		2		1	1	1	
Ptilidium ciliare	2		1	1	1	2	2	4	3	2
Cladonia furcata										1
C.impexa										1
C.sylvatica										
B) PODSOL-FAVOURING										
Agrostis tenuis	1	1	1	2	1	1				
Carex bigelowii	2				1		1	3	1	1
C.caryophyllea										
Galium saxatile	2	1	2	3	3	1			1	
Vaccinium myrtillus	2	1	1	1	1	1			1	
Hypnum cupressiforme	2								2	
Hylocomium splendens										
Mnium hornum										
Rhytidiadelphus squarr.	3	3	3	3	2	1	2	1	1	
Lophozia floerkii		1	1		2	2	2	2	2	
L.lycopodioides	1		1				1	1		
Cetraria islandica										
C) PEATY-GLEY FAVOURING										
Carex nigra										
Potentilla erecta										
Rhytidiadelphus loreus						2				
Sphagnum cuspidatum										
S.recurvum										
Calypogeia trichomanis							2		2	1
Diplophyllum albicans							1			
D) BLANKET-BOG FAVOURING										
Eriophorum angustifolium										
E.vaginatum										
Calluna vulgaris										
Empetrum nigrum										
Aulacomnium palustre										
Sphagnum plumulosum										

Quadrat number	S1	S2	S3	S4	S5	S6	S7	S8	S9	Sx
A) OVERALL										
Agrostis canina				1	1			1		
A.stolonifera							1			
Deschampsia flexuosa	5	4	4	5	4	4	3	4	4	5
Festuca ovina			2	3	3	4	4	2	4	5
Juncus effusus										
J.squarrosus	8	8	8	8	7	8	8	8	8	7
Luzula campestris										
Nardus stricta			1	1		1		1		
Dicranum scoparium	1	1	2			2			2	1
Plagiothecium undulatum							2	1	3	2
Pleurozium schreberi			1			2	1	1	1	1
Polytrichum alpinum										
P.commune	4	5	4	5	5	5	5	5	5	4
Splachnum ovatum										1
Lepidozia reptans									1	
Lophocolea bidentata		3	2	1		2	2	2	2	2
Lophozia ventricosa						1	1	2		
Ptilidium ciliare	1	1	1	2		1			1	
Cladonia furcata										
C.impexa										
C.sylvatica						1				
B) PODSOL-FAVOURING										
Agrostis tenuis										
Carex bigelowii										
C.caryophyllea										
Galium saxatile						1	1	1		
Vaccinium myrtillus	2	1	2			2	1	1	2	1
Hypnum cupressiforme	2	1	2	2	1	2	2	1		
Hylocomium splendens										
Mnium hornum										
Rhytidiadelphus squarr.					1	1		1		1
Lophozia floerkii		1	1			2	2	3		
L.lycopodioides										
Cetraria islandica										
C) PEATY-GLEY FAVOURING										
Carex nigra	1	1	2		1	1			1	2
Potentilla erecta	1		1	1	1	1	1	2		1
Rhytidiadelphus loreus	1	1	2	2	1	2	2	2	3	2
Sphagnum cuspidatum	2	1						2		
S.recurvum					3		2	1		
Calypogeia trichomanis		2	1	2	1	1	1	1		1
Diplophyllum albicans	3	1					2	2		
D) BLANKET-BOG FAVOURING										
Eriophorum angustifolium										
E.vaginatum										
Calluna vulgaris										
Empetrum nigrum										
Aulacomnium palustre										
Sphagnum plumulosum										

Quadrat number	H1	H2	H3	H4	H5	H6	H7	H8	W1	W2	W3	W4	W5	W6	W7	W8	W9
A) OVERALL																	
Agrostis canina				2			1										
A.stolonifera																	
Deschampsia flexuosa	1	1	x		2	1		1	2	1		1		2	1	2	1
Festuca ovina	4	6	5	4	5	5	5	5					2			2	
Juncus effusus			2														
J.squarrosus	7	7	7	8	8	7	6	7	4	3	4	6	6	2	2	3	1
Luzula campestris	1						1									1	
Nardus stricta			4					1									
Dicranum scoparium	2																
Plagiothecium undulatum			3	3		2			2		2	2	5	2			
Pleurozium schreberi									1	4	2			3	2	2	1
Polytrichum alpinum																	
P.commune	3	3	3	4	4	4	5	4	x	1	2	4	3	5	4	3	1
Splachnum ovatum		x															
Lepidozia reptans											1						
Lophocolea bidentata	2	3		1	2	x	x	2	2	1	1		2	1	1		
Lophozia ventricosa			x	1							1						
Ptilidium ciliare	1		1		1		1			1	1	1	1	2	1		
Cladonia furcata																	
C.impexa																	
C.sylvatica																	
B) PODSOL-FAVOURING																	
Agrostis tenuis		1		2													
Carex bigelowii																	
C.caryophyllea																	
Galium saxatile		1	1	1			4										
Vaccinium myrtillus																	
Hypnum cupressiforme							x										1
Hylocomium splendens																	
Mnium hornum																	
Rhytidiadelphus squarr.			2				1	1	1				1			1	
Lophozia floerkii												2					
L.lycopodioides																	
Cetraria islandica																	
C) PEATY-GLEY FAVOURING																	
Carex nigra	2	2	2	2		3	3								1	1	
Potentilla erecta				1		x	1										
Rhytidiadelphus loreus									1	2	2	2	1	1	2		
Sphagnum cuspidatum																	
S.recurvum				5		5	4										
Calypogeia trichomanis	2	2	1	2	1	2	1		2	2	3	2	2	1	2	2	
Diplophyllum albicans																	
D) BLANKET-BOG FAVOURING																	
Eriophorum angustifolium	1	x		1		2		1	1	1	2	1	2	1	3	2	2
E.vaginatum	5	4	4				4		6	4	5	4	2	5	4	7	4
Calluna vulgaris					x				6	8	8	6	7	5	8	6	7
Empetrum nigrum											2	2		1	1		x
Aulacomnium palustre	2	1		1	x			2				2				2	
Sphagnum plumulosum									4	4	4	2	3	2	4	5	7

Plate 5 - Section 6: Peaty gley nodum on slopes below _Calluna_ - _Eriophorum_ blanket bog. (Site H quadrats were done in the foreground and on the slope in the middle right).

Plate 6 - Section 6: Another view of a stand of the peaty gley nodum, (this containing some _Juncus effusus_).

characteristic species including Eriophorum vaginatum, Acrocladium stramineum, Rhytidiadelphus loreus, Sphagnum cuspidatum, S. plumulosum, S. recurvum and Diplophyllum albicans.

Table 6.4 shows the transitions between this nodum and the podsol (peaty podsol facies) on the one hand and blanket bog on the other. In some cases stands belonging to the nodum have obviously resulted from biotic change of blanket bog, e.g. the O quadrats which are on old pony tracks made in the lead mining days. But these often link larger patches of Juncus squarrosus on slopes below blanket bog where thin bands of limestone outcrop (quadrats H, see Plates 5 and 6), and here it appears that Juncus squarrosus is the primary vegetation. As the slope lessens the depth of peat gradually increases, and the community passes into Calluna - Eriophorum - Sphagnum blanket bog. The presence or absence of Eriophorum vaginatum is controlled by depth of peat, whereas Calluna is controlled more by climate - it is rare above 2,250 ft. on the Reserve - and sheep grazing, as will be discussed later. Suffice to say that conditions at many of the peaty gley sites would favour Calluna, especially on the west side of the Reserve, but here grazing pressure is more severe and winter grazing has very probably been long-continued.

The *Juncus squarrosus* community in high-level blanket peat dominated by *Eriophorum vaginatum* at 2300 ft. at Rough Sike Head.

	1	2	3	4	5	6	7	8	9	10
Deschampsia flexuosa		2	2	2	2		2	1		
Eriophorum angustifolium	1	3	2	2	1		1	2		1
E. vaginatum	7	4	1	5	4	5	4	5	4	5
Festuca ovina	2	1	1	1		2	2			
Nardus stricta		1					1	1	4	
Rubus chamaemorus	x									
Vaccinium myrtillus								1		
Campylopus pyriformis								1		
Calypogeia trichomanis	1	3	1	1		1		1		
Diplophyllum albicans	2	2	1	1	2	2		1	5	4
Ptilidium ciliare	x			3	1		1			1
Cladonia cornuta					x					
C. furcata								1		
C. impexa								1		
Algae					1					

Plate 7 - A wide expanse of the peaty gley nodum at 2500 ft. (The slope behind has patches of *Nardus stricta*).

Above the _Calluna_ limit, _Eriophorum_-dominated blanket bogs frequently show sheet erosion (Bower's second type (1959), and here _Juncus squarrosus_ often invades in ring patches. 10 quadrats done at Rough Sike Head in such patches do not easily fit into the peaty gley nodum, but are given separately (Table 6.5). There are very few species, and _Diplophyllum albicans_ is especially characteristic. On shallower peat and peaty gleys (H layer 20-50 cms.) from 2,400 ft. upwards, stands of _Juncus squarrosus_ belonging to this nodum cover much ground in the Moor House area (Plate 7).

Species-poor gley nodum (Table 6.6)

Only 16 lists were found belonging to this nodum, all but one being from alluvial grasslands. They contain 48 species, contrasting with 88 in the 31 quadrats of the species-rich gley nodum. Lichens are almost absent, but there are more herbs, chiefly _Galium saxatile_, than in the peaty gley nodum, as the sward is more grassy, and _Juncus squarrosus_ usually shares dominance with _Festuca ovina_ and _Nardus stricta_.

The nodum has 8 constants. Besides _Festuca ovina_ and _Lophocolea bidentata_, these comprise _Agrostis tenuis_, _Luzula campestris_, _Nardus stricta_, also constants in the species-rich gley nodum, but less frequent in the podsol nodum; _Galium saxatile_ and _Rhytidiadelphus squarrosus_, constants in the species-rich gley and the podsol noda; and lastly _Hypnum_

SPECIES-POOR GLEY NODUM

$4m^2$ quadrats I $\frac{1}{4}m^2$ quadrats - - - - -

Site	Trout Beck Foot alluvium			Nether Hearth Sike all.			Moss Burn alluvial				Dipper drift	Trout Beck Foot alluvial							
Altitude (feet)	1750			1850			1850				150	1750							
Quadrat number	1	2	3	C1	C2	C4	C6	C7	C9	Cx	F7	B1	B2	B3	B4	B7	B8	B11	B12
Slope (degrees)			1		1		2		2	1	4								
Aspect			NE		NW		NE		SE	E	NE								
Agrostis canina	1			2	3	1		x				2		1					
A. tenuis	4	3	3			3	2		2	1	2	4	3	4	2	4	4	4	4
Anthoxanthum odoratum	3	3	2			1	1		2		1		1		1			1	
Carex nigra				2		2	1	1		2									
Deschampsia cespitosa			2																
D. flexuosa					1					2	2								
Festuca ovina	7	6	7	3	5	4	4	4	4	4	4	5	7	5	5	5	6	6	6
J. squarrosus	6	8	7	7	7	6	5	8	7	6	4	8	5	8	7	7	7	7	7
Luzula campestris	3	2	3	1			2	1	1		2	2	1	1	1	1	2	2	2
Molinia caerulea											1								
Nardus stricta	3	3	2	5	1	6	6	5	6	7	5		4	3	3	1			2
Achillea millefolium																x			
Cardamine pratensis																1			
Cerastium holosteoides																1			
Galium saxatile	2	3	2	1	5	4	3	1	3		4	3	4	3	3	2	4	3	3
Narthecium ossifragum										1									
Potentilla erecta						2	2		2	1	3								
Rumex acetosella			1																
Viola palustris						x	1		2										
Atrichum undulatum												2	x						
Barbula recurvirostra																1			
Dicranum scoparium		1	1								1		x		2				1
Eurynchium praelongum												x							
Hylocomium splendens	3	2	2						1		2	3	2	1	2	2	3	2	2
Hypnum cupressiforme	3	2	2	2	1	2	2	4	2	1	2	1		2	2	1	1	2	1
Mnium hornum	2	1		1					1									1	1
Plagiothecium undulatum				2	1		2	1		x			2		2	1	1		
Pleurozium schreberi	3	2	1	1		1			1		1							1	1
Pohlia nutans													x						1
Polytrichum commune				2	3		5	2											
P. juniperinum	x														x				
Pseudoscleropodium purum						x	1		2		1								
Rhytidiadelphus squarrosus	3	3	3	2	2	2	2	x	2	x	2	2	2	2	2	2	2	3	2
Sphagnum palustre				4	x					x									
Thuidium tamariscimum						x													
Calypogeia trichomanis	x	1	1	2			1	3							x	1			1
Lepidozia reptans																1			
Leptoscyphus taylori						x				x									
Lophocolea bidentata	2	2	2	2	2	x	4		1		2	2		1	3	2	2	1	1
Lophozia barbata												1			1			2	2
L. floerkii	1	1				x													1
L. lycopodioides	1																		
L. ventricosa	x																		
Pellia sp.				1															
Ptilidium ciliare				2	1			1											
Scapania gracilis												x						1	
Cladonia furcata	1																		1
Peltidea aphthosa				1															

Table 6.7

SPECIES-RICH TO SPECIES-POOR GLEY GRADIENT

	species-rich gley	species-poor gley
Sites as in Tables 6.6 and 6.8	X X X X X X X X X X D D D B B B C C D F F F F B D D C D D D D	B C C C F C C C C B B B B B B B H H
Quadrat number	1 2 3 4 5 6 7 8 9 x x 1 3 6 9 x 3 8 9 1 2 3 4 5 7 5 5 2 6 8 4	7 4 6 9 7 1 2 x 7 1 2 3 4 8 11 12 9 x
A)THROUGHOUT		
Agrostis canina	1 1 1 2 1 1	1 2 3 x 2 1
Agrostis tenuis	5 5 4 4 3 3 3 2 3 4 2 2 2 3 4 3 3 3 2 5 3 4 3 1 1 2 2 2 2 2 3	4 3 2 2 2 1 4 3 4 2 4 4 4 2
Carex nigra	1 1 1 3 1 1 2 1 1 1 1 1	2 1 2 2 1 3 2
Festuca ovina	6 4 5 6 5 7 6 7 6 5 5 5 6 4 5 6 4 7 6 5 3 5 7 6 6 5 3 6 6 5 5	5 4 2 4 4 3 5 4 4 5 7 5 5 6 6 6 7 5
Juncus effusus	1 2 1 1 2 5 2 3 2 1 2 1	x x
J.squarrosus	5 6 6 7 5 7 6 6 5 6 6 4 4 8 8 7 6 8 6 5 3 5 7 6 6 5 6 5 6 6 6	7 6 5 7 4 7 7 6 8 8 5 8 7 7 7 7 7 7
Luzula campestris	2 2 2 3 1 2 2 3 1 1 1 1 1 2 x 2 1 211 3 2 1 1 1 1 2 1 1	1 2 1 2 1 2 1 1 1 2 2 2
Nardus stricta	5 6 5 2 7 3 4 5 4 3 5 5 5 1 6 2 5 4 2 6 2 4 7 5 6 5 5 4	1 6 6 6 5 5 1 7 5 4 3 3 2
Galium saxatile	3 3 2 2 2 2 3 2 2 3 3 1 2 3 2 3 3 2 3 4 2 2 2 3 3 2 2 2	2 4 3 3 4 1 5 1 3 4 3 3 4 3 3 5 4
Narthecium ossifragum		1
Barbula recurvirostra		1
Dicranum scoparium	1 2 1	1 x 2 1
Hylocomium splendens	- - 3 3 3 1 3 1 - 2 2 2 1 3 2 3 - . 1 2 - - 1 2 1 - - - - - 1	2 - - 1 2 - - - - 3 2 1 2 3 2 2 - -
Hypnum cupressiforme	3 1 - 1 4 - 1 - 1 - - 1 1 2 1 1 2 2 1 3 - 1 3 2 2 - 1 - 1 1 1	1 2 2 2 2 2 1 1 4 1 2 2 1 2 1 3
Mnium hornum	2	1 1 1 1
M.pseudopunctatum	1	
Pleurozium schreberi	3 1 2 1 1 1 1 1 2 1 1 1 1	1 1 1 1 1 1
Pohlia nutans	1 1	x
Polytrichum commune	1 2 1 2 4 2 1 2 1	5 2 3 2 1
P.juniperinum	1	x
Pseudoscleropodium purum	2 3 1 1 x 1 1	x 1 2 1
Rhytidiadelphus squarrosus	4 1 3 1 1 2 2 4 3 1 3 2 3 1 2 2 1 3 2 1 2 3 2 1 2 1 1 1 3	2 2 2 2 2 2 2 x x 2 2 2 2 2 3 2 4 4
Splachnum ovatum	1	
Leptoscyphus taylori	1 1 1 1	1 x x
Lophocolea bidentata	2 1 2 1 2 2 2 2 1 1 1 3 2 3 2 1 2 1 1 1 2 3 1 2 1 1 2 1 2	2 x 4 1 2 2 2 2 1 3 2 1 1 1 2
Lophozia barbata	1	1
L.floerkii	1 1 1 1	x 2 2
L.lycopodioides		1
L.ventricosa	1	
Pellia sp.		1
Ptilidium ciliare	1 1 1 1 1 3 1	2 1 1
Scapania gracilis	x 1 1	1
B)SPECIES-RICH GLEY SPECIES		
Anthoxanthum odoratum	2 2 4 4 2 3 3 3 3 3 1 2 1 1 1 3 2 1 1 3 1 1 1 2 2 1	1 1 2 1 1 1 1
Carex demissa	1 1 2 1 1 1 1 1 1	
C.flacca	1 1 2 2 1 1 1 1 1 1 1 1 1	
C.ovalis	1	
C.panicea	2 2 1	
C.pulicaris	1 1 1 1 3 2 1	
Cynosurus cristatus	1 2 1	
Deschampsia cespitosa	1 1 1	
Festuca rubra	2 3 1 2 1 1 2	
Holcus lanatus	2 1 1	
Poa pratensis	1 1 1 1 1	
Achillea millefolium	1 2 2 2	x
A.ptarmica	3 2 3 2 3 1 2 2	
Bellis perennis	2 1	
Cardamine pratensis	1 1 x 1 1 x 1 x	1
Cerastium holosteoides	1 1 1 2 1 1 1 1 2 x 1	1
Cirsium palustre	1 1 x 1 1 1 1 2 1 1 1	
Equisetum palustre	1 1 1 - 1 2 1 1 1 - 1 1 - 1 1 1 - - - - x - - - - - 1 - - - -	(
Euphrasia sp.	1 1 x x	
Hieracium pilosella	2 1 1 1	
Leontodon autumnalis	2	
Plantago lanceolata	1 1 1 1 1 1 2 2	
Polygala serpyllifolia	2 2 3 1 2 1 2 1 1 2 3 1 2	
Potentilla erecta	1 1 2 3 3 2 2 3 2 3 1 x 1 4 1 2 2 2 2 3 3 1	2 2 2 3 1
Prunella vulgaris	2 3 2 1 1 2 2	
Ranunculus acris	3 x 1 1 2 1	
R.flammula	1	
Rumex acetosella	1 2 3 2	
Selaginella selaginoides	1 x 1	
Taraxacum officinale	1 1 x 1 1	
Thymus drucei	4 1 3 3 2 1	
Trifolium repens	4 3 4 - - 2 4 2 - 3 - 3 3 2 2 2 3 3 2 - 2 1 - 3 2 - 3 3 - - -	
Veronica officinalis	1 1	
V.serpyllifolia	2 2 1 x 2 2 1 1	x 1 2
Viola palustris	2 1	
V.riviniana	1 2 2 2 1 1	
Acrocladium cuspidatum	2 1 1 2 3 3 2	
Atrichum undulatum	1 1 1 1 2 1 x 1	2 x
Aulacomnium palustre	x 1 4 1 1 2 2	
Climacium dendroides	2 1	
Ctenidium molluscum	1 2	x
Eurynchium praelongum	2 2 3 3 1	
Mnium longirostrum	1 1	
M.punctatum	1 1 2 1	
M.undulatum	1 1 1 1 2 1	
Rhodobryum roseum	x	
Thuidium tamariscinum	x x 2 1 1 1	x
C)SPECIES-POOR GLEY SPECIES	x	2 1 2 1
Deschampsia flexuosa		1
Molinia caerulea		1 - 2 - - - 2 1 x 1 - - - 2 2 1 - - - 2
Plagiothecium undulatum	1	4 x x
Sphagnum palustre	x 2 2	1 1 2 3 x
Calypogeia trichomanis		1
Lepidozia reptans		

cupressiforme, which is near-constant in the other two noda. Neither are the two near-constants characteristic, Plagiothecium undulatum being a near-constant in the peaty gley nodum, and Hylocomium splendens a near-constant in the species-rich gley nodum. There are no characteristic species of lesser frequency, so that, as with the podsol nodum, this nodum is recognised by the distinctive combination of species present and the rarity of others, e.g. Deschampsia flexuosa, Polytrichum commune and Lophozia floerkii frequent in allied noda.

Though this nodum has not a great acreage on the Moor House reserve, it is widespread on the eastern side, being the typical community found on the peaty silts laid down in narrow strips by the streams (called becks, burns or sikes) flowing through the blanket bog. In some places it grades to Festucetum, usually where more recent and gravelly alluvium has been deposited, in others to pure Nardetum, but this is much less common. Where the water is more basic, the stands, especially close to a stream, contain more species, grading to the species-rich gley nodum as shown in Table 6.7. At the valley side the species-poor gley nodum passes laterally almost everywhere into the peaty gley nodum, which in turn passes into blanket bog.

Eddy does not map the nodum, because of its small extent, but includes it in his alluvial grassland unit, together with pure Festucetum and Nardetum.

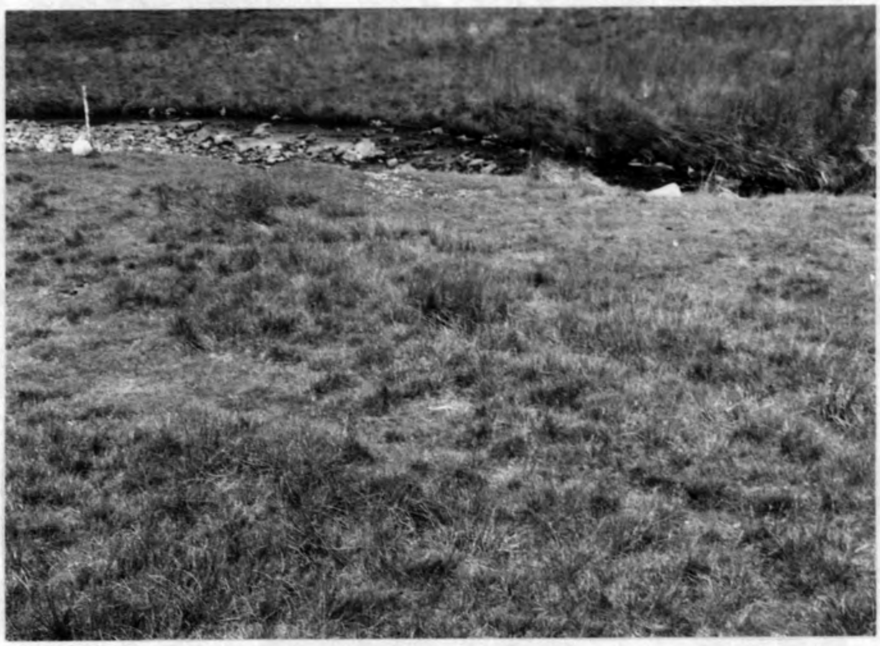


Plate 8 - A stand of the species-poor gley nodum on an alluvial terrace besides Nether Hearth Sike.

Table 6.8

$4m^2$ quadrats I $\frac{1}{4}m^2$ quadrats - - SPECIES-RICH GLEY NODUM

Site and Altitude (feet)	Trout B. green slopes 1800			Trout Beck green slopes. 1850										Trout B.Foot 1750				Moss Burn 1850			Trout Beck leat 1775										Dipper flushed shallow soil 1550			
Quadrat number	1	2	3	X1	X2	X3	X4	X5	X6	X7	X8	X9	Xx	B5	B6	B9	Bx	C3	C5	C8	D1	D2	D3	D4	D5	D6	D7	D8	D9	Dx	F1	F2	F3	F4
Slope and Aspect	3S	3S	3S	3S	5S	6SW	4S	2S	2S	2S	3S	2S	3S	-	2SE	-	-	1W	-	-	7S	8S	5S	3S	5S	6S	6S	-	4S	4S	2SE	1E	5E	3NE
Agrostis canina		1										1		1				1				2	1			1		1						
Agrostis tenuis	4	4	4	5	5	4	4	3	3	3	2	3	4	1	3	4	3	3	2	3	2	2	2	3	2	2	1	2	2	2	5	3	4	3
Anthoxanthum odoratum	2	2	2	2	2	4	4	2	3	3	3	3	3			1	1	3	2	2	2	2	1		1		1	1		1	1	1	3	1
Carex caryophyllea	1	1	1																															
C.demissa		1																			1	1		1	1	1	1	1	2	1				
C.flacca	1	1		1	1	2			2	1	1	1	1						1	1	1	1	1	1	1	1	1	1						
C.nigra	3	1	1	1		1		1	3	1	1	2							1	1	1	1	1					1					1	
C.ovalis	1	1			1																													
C.panicea		2	1		2			2			1																							
C.pulicaris	2	3	3		1						1										1		3		1		2			1				
Cynosurus cristatus																															1	2		1
Deschampsia cespitosa								1		1																			1					
D.flexuosa																			x															
Festuca ovina	6	5	5	6	4	5	6	5	7	6	7	6	5	6	4	5	6	4	3	7	5	6	6	5	5	6	6	5	6	5	5	3	5	7
F.rubra	1		1	2	3	1	2			1		1	2																					
Holcus lanatus		3	2		2	1					1																			1		1		
Juncus effusus	1	1	3	1		2	1	1		2		5	2						2	3				1	1				2					
J.squarrosus	6	5	5	5	6	6	7	5	7	6	6	5	6	7	8	8	7	6	6	8	4	5	4	7	5	6	5	6	6	6	4	6	6	6
Luzula campestris	3	2	3	2		2		2	3	1	2	2	3		1	1	2	x	1	2	1	1	1	1	1	2	1	1	1	1	2	1	3	2
Nardus stricta	6	6	6	5	6	5	2	7	3	4	5	4	3				1	6	5	2	5	6	5	4	7	5	4	5	5	5	4	2	6	2
Poa pratensis	1	1	1	1	1		1														1												1	
Sieglingia decumbens																															1			1
Achillea millefolium														2	1	2	2																	
A.ptarmica		1		3										2	2	3					3	2							1	2				
Bellis perennis				2																	1													
Cardamine pratensis	1	2	1		1										1	1		x		1	1	x	x											
Cerastium holosteoides	1	1	2	1	1		1		2		1									2	1		1					1		1			x	1
Cirsium palustre	2	2	1		1	1		x		1	1		1								1		2	1				1		1				
Empetrum nigrum		1																																
Epilobium anagallidifolium			1																															
Equisetum palustre	1	1	1	1	1	1		1	2	1	1	1			1	1	1				1				1					1		x		
Euphrasia sp.	1	1																	x		1									1			x	
Galium saxatile	3	2	2	3	3	2		2	2	2	3	2	2	2	3	1	2	3	3	2	3	3		2	2	2	2	3	3		3	2	3	4
Hieracium pilosella						2		1	1																						1			
Leontodon autumnalis							2																											
Plantago lanceolata					1		1	1		1	1									1											2	2		
Polygala serpyllifolia	1	2	2				2			2	3	1	2					1			2		1	2	3	1	2	2		1				
Potentilla erecta	3	4	3	1	1	2	3	2	2	2	3	2	3		x		1	4	1	1		1		3	3	3	1	3	2	1		2	2	2
Prunella vulgaris	1	2	1	2	3		2	1												2			2							1				
Ranunculus acris	1	2	2	3														x		1							1		1			2		
R.flammula		1																												1				
Rumex acetosella			2			1					2	3																			2			
Selaginella selaginoides		2																									1		x	1				
Taraxacum officinale	1	1	1				1																				1			1	x	1		
Thymus drucei							4	1						1		3	3			2														
Trifolium repens	4		3	4	3	4			2	4	2		3	3	2	2	2	3	3	3	3	3	3				2		2			2	1	
Veronica chamaedrys			1																															
V.officinale											1																							
V.serpyllifolia			1																		1													
Viola palustris		1												2		2	2	1	1	x							1		2					
V.riviniana	2	2	1		1		2		2	2							2						1				1			1				
Acrocladium cuspidatum				2			1																							1	2	3		
A.stramineum			1																															
Atrichum undulatum	2		1						1	1				3	1	2	1		x		1							1				2		
Aulacomnium palustre	2	2	2			x	1						4									1			1	2		2						
Climacium dendroides					2																1													
Ctenidium molluscum					1																									2				
Dicranum scoparium						1							2																					1
Eurynchium praelongum																													2		2	3	3	1
Hylocomium splendens	4	4	3			3	3	3	1	3	1		2	2	3	2	3				2		1	1			1		1	2	2			1
Hypnum cupressiforme			2	3	1		1	4		1		1		2	2	1	1	2	1	2	1		1	1		1	2	1	1		3		1	3
Mnium hornum																		2																
M.longirostrum					1								1																			1		
M.pseudopunctatum																			1															
M.punctatum	1	1	1					1								2											1		1	1				
M.undulatum	2	2	2				1	1	1	1													2					2	1					
Pleurozium schreberi	2								1					1	2		1	1			2	1	2	1		1	1							1
Pohlia nutans																			1			1												
Polytrichum alpinum		1													x																			
P.commune	4																	2	4		1	2		1	2	1		2	1					
P.juniperinum			1														1		1															
Pseudoscleropodium purum			2						2			3							1	1								1			1	x		
Rhodobryum roseum																x																		
Rhytidiadelphus squarrosus	5	4	4	4	1	3	1	1	2	2	4	3	1	1	1	2	2	1	1	3	2	1	3	3	2			1	2	3	1	2	3	2
R.triquetrus														2																				
Sphagnum palustre																			1															
S.plumulosum																												4						
Splachnum ovatum																																1		
Thuidium tamariscinum	1	1	2			1	4	2	2	1	1		1					x		x		1			1		2	1		1				
Calypogeia trichomanis																						x				21		2		1				
Leptoscyphus taylori	1						1	1		1							1																	
Lophocolea bidentata	3	2	2		2	1	2	1	2	2	2		1	1	2	3	2	1	1	2	1	x	3	2	1		2	1	1	2	1	1	2	3
Lophozia barbata								1																										
L.floerkii	1							1							1							1						1						
L.ventricosa																1																		
Ptilidium ciliare	1	2						1					1									3			1	1	1							
Scaparia gracilis				x	1				1																									

Species-rich gley nodum (Table 6.8)

31 lists from 5 sites have been placed in the species-rich gley nodum. In comparison with species-poor gleys, herbs and sedges are much more abundant, and there are more mosses but fewer liverworts. Lichens again are almost absent. _Juncus squarrosus_ is usually more a community member than a dominant, and the sward of _Festuca ovina_ and _Nardus stricta_ is often well grazed down. Even _Juncus squarrosus_ is considerably grazed here, e.g. 32.4% of the inflorescences were eaten at site D in 1962.

The nodum has 9 constants and 4 near-constants. _Potentilla erecta_ is the only characteristic constant, the rest being constants elsewhere, _Anthoxanthum odoratum_ in the flushed-peat nodum, and _Agrostis tenuis_, _Festuca ovina_, _Luzula campestris_, _Nardus stricta_, _Galium saxatile_, _Rhytidiadelphus squarrosus_ and _Lophocolea bidentata_ in the species-poor gley nodum and others. Of the near-constants, _Equisetum palustre_ and _Trifolium repens_ are also near-constants in the flushed-peat nodum, and _Hylocomium splendens_ and _Hypnum cupressiforme_ are constants in the species-poor gley and podsol noda respectively. Characteristic species include _Poa pratensis_, _Juncus effusus_, _Hieracium pilosella_, _Plantago lanceolata_, _Polygala serpyllifolia_, _Thymus drucei_, _Atrichum undulatum_ and _Thuidium tamarascinum_.

FLUSHED-PEAT NODUM

Site	$4m^2$ quadrats I Moss Burn			$\frac{1}{4}m^2$ quadrats Pasture		Moss Burn			Hard Hill				Trout Beck		
Altitude (feet)	2100			1800		2100			2150				1800		
Quadrat number	1	2	3	M1	M2	M4	M5	M6	M8	M9	M10	M11	M13	M14	M15
Aspect	N	N	N	SW	SW	-	N	N	SE	SE	SE	SE	E	E	SE
Slope	4	4	4	3	3		5	4	4	4	4	3	1	2	1
Agrostis canina										1					
A.stolonifera		2						2						1	1
A.tenuis			1								1	1	2	2	
Anthoxanthum odoratum	2	3	3		1	1	2		2	3	2	2	2	3	3
Briza media												1			
Carex curta						1			1	2	1			1	1
C.demissa	1		2	2			1		1					2	
C.dioica	1							1					1		
C.echinata			1										1	1	1
C.flacca	3	1	2	2	2		1								
C.nigra	2	2	5	4	5	3	2	2	7	6	5	4	4	2	3
C.panicea		2				2	2							1	
C.pulicaris	2	2	1			1		2							
Deschampsia cespitosa	3	1	2	2			2					3			
Eriophorum angustifolium			1	1	1	1	1	2		1	1	1	1		
E.vaginatum									1						
Festuca ovina	5	4	2	3	1	1	4	1	4	2	2	2	4	3	3
F.rubra	4	3	3	5	5	2	3	2	3	3	4	5	2		1
Holcus lanatus	1	1	1												
Juncus articulatus	1		1						1				1		
J.bulbosus						2	1							2	
J.effusus									1				1	2	1
J.kochii		1	2												
J.squarrosus	7	7	6	7	5	6	6	5	6	5	6	6	6	5	6
Luzula campestris	1	1	1						1		1		1	2	
Nardus stricta	4	6	4		4	2	3	3	2	2	2		2	5	2
Achillea ptarmica								1							
Alchemilla glabra		1													
A.vestita	2														
Bellis perennis	2	2	1				2								
Caltha palustris			1					1							
Cardamine pratensis	1	2	3		1	1		1	2	3	2	2	3		2
Cerastium holosteoides		2	1		1			2	1	1	1	1	1		1
Cirsium palustre		1	1					1							
Empetrum nigrum	5														
Epilobium anagallidifolium	x	2	2		1	x	1	1	1	1	1	2	1		
Equisetum palustre	1	1	2	1	2		1	1					2		1
Euphrasia sp.	1	2				1									
Fragaria vesca									1						
Galium palustre		1	1			2	2	1	1	2	1	1	2		1
G.saxatile									1						2
Geum rivale	1														
Leontodon autumnalis	3	3	1	2	3		2	1							
Montia sp.						x									
Parnassia palustris	1		1				1								
Potentilla erecta	2	3	1				1		2		2			2	
Prunella vulgaris	3	3				1	1	1							

	1	2	3	M1	M2	M4	M5	M6	M8	M9	M10	M11	M13	M14	M15
Ranunculus flammula		1	2			1		2							
R.repens	2			1											
Rumex acetosella									2		1				
Sagina procumbens		1	1						1	1					1
Sedum villosum			1												
Selaginella selaginoides	2	2	2				1	1	1						
Taraxacum officinale			1												
Trifolium repens	2	2	3			1		2	2	2			3	1	2
Triglochin palustris		1										1			
Veronica anagallis-aquatica		1													
V.serpyllifolia											1	1			
Viola palustris			2			1		1			1			2	2
V.riviniana	2	2					2								1
Acrocladium cordifolium											1				
A.cuspidatum	4	4	4	3	3	1	2	2	2	3	2		3	2	
A.stramineum					1								1		
Brachythecium rivulare						1									
Bryum pseudotriquetrum	1	2	3		3		1	2	2	3	1	2			
Campylium stellatum	3	3	1												
Cratoneuron commutatum							1								
Ctenidium molluscum	3	3						2							
Drepanocladus aduncus						2									
D.revolvens			3												
Fissidens adianthoides						1		1							
F.osmundoides	3	3	3												
Hylocomium splendens		1	x	3	3		1								3
Hypnum cupressiforme				1			1								
Mnium hornum	1	1	2												
M.punctatum	2	4	3	4	5	1	1	2	5	4	3		2		2
M.undulatum	1	2	3					1			1	1	1		1
Oncophorus virens	1	1													
Philonotis fontana	1	2	2	2	3	2	1	2			1	1			
Polytrichum commune													1	1	
P.juniperinum		1													
Rhytidiadelphus squarrosus				1	1					1	1	5	2	2	3
R.triquetrus	1	1													
Thamnium alopecurum										1	1	2			
Thuidium tamariscinum		2													
Sphagnum palustre															1
S.plumulosum													1		
Aneura pinguis		1	1	1	1	1		2	1		1				
Leptoscyphus taylori	1	1	1				1								
Lophocolea bidentata	2	1		3	3	1	2	2		1		2	1	2	2
Lophozia bantriensis		2													
L.quinquedentata	1	1													
Pellia spp.									1		1				
Scapania gracilis														3	
S.irrigua	3	3	2				3								

This nodum covers about the same area on the Moor House Reserve as the species-poor gley, but only a few of the stands are on alluvium. Most are found on drift slopes at the sides of the deeper valleys, frequently below limestone outcrops, so that they are irrigated by water, acid from the blanket bog above, which has picked up some bases. Eddy does not map the nodum as such, but shows it on his map as an Agrosto-Festucetum with a stippling of dots of the Nardetum colour, and additionally he distinguishes it in his association tables as a bryophyte-rich facies of Nardetum sub-alpinum. Away from base-rich irrigation, the nodum grades into the peaty gley, whilst in very wet places peat develops, and it grades into the flushed-peat nodum.

The flushed-peat nodum (Table 6.9)

This nodum has more species than any other, but it is the least extensive and is not mapped by Eddy. However, it is the typical marginal community separating calcareous flushes from the surrounding blanket bog. In some flushes where grazing is heavy Juncus squarrosus invades the sward forming ring patches, which usually have a rich flora, including Saxifraga hirculus at one place, though no quadrats were done there. Such stands are at the base-rich extreme of the ecocline (Table 6.10) which passes to blanket bog at its other. Whilst the very rich stands of Juncus squarrosus probably owe their

FLUSHED-PEAT TO PEATY GLEY GRADIENT

Sites M1,2 = Pasture, Moor House at 1850', M12,13 = Trout Beck at roadbridge, 1750',
M3 - 6 =Moss Burn flush, 2100', M14=Trout Beck gorge, 1800', M15=Nether Hearth Sike, 1800',
M7 - 11 = Hard Hill flushes, 2150', H1 - 7 = Teesside green slopes, 1800'.

Quadrat number	M6	M5	Mx	M15	M4	M2	M8	M9	M13	M11	M1	M14	M3	M7	M12	H1	H2	H3	H4	H5	H6	H7
Aspect	N	N	SE	SE	-	SW	SE	SE	E	SE	SW	E	N	SE	W	E	E	E	E	E	SE	SE
Slope (degrees)	4	5	4	1		3	4	4	1	3	3	2	1	4	1	5	5	5	8	5	1	3
A) OVERALL SPECIES																						
Agrostis canina								1											2			1
A.stolonifera	2			1		2						1	2	1								
A.tenuis			1						2	1		2					1		2			
Briza media										1												
Carex echinata				1					1			1	1		1							
C.nigra	2	2	5	3	3	5	7	6	4	4	4	2	3	6	5	2	2	2	2		3	3
Eriophorum angustifolium	2	1	1		1	1		1	1	1	1		1		4	1	x		1		2	
Festuca ovina	1	4	2	5	1	1	4	2	4	2	3	3	2	5	5	4	6	5	4	5	5	5
Juncus articulatus							1		1						1							
J.effusus				1			1		1			2		2				2				
J.squarrosus	5	6	6	6	6	5	6	5	6	6	7	5	5	5	5	7	7	8	8	8	7	6
Luzula campestris			1				1		1			2	1			1						1
Potentilla erecta		1	2				2					2	2						1		x	1
Acrocladium stramineum			x			1			1				3									
Drepanocladus fluitans														1								
Hypnum cupressiforme		1									1											x
Rhytidiadelphus squarrosus			1	3		1		1	2	5	1	2	1					2				1
Sphagnum palustre				1											2							
S.plumulosum									1				1									
Leptoscyphus taylori		1																				
Lophocolea bidentata	2	2		2	1	3		1	1	2	3	2	2	3		2	3		1	2	x	x
Scapania gracilis												3										
S.irrigua		3											2	1								
B) RICH-FLUSH SPECIES																						
Carex dioica	1								1													
C.pulicaris	2				1																	
Achillea ptarmica	1				1																	
Bellis perennis		2																				
Caltha palustris	1																					
Cardamine pratensis	1		2	2	1	1	2	3	3	2												
Cerastium holosteoides	2		1	1		1	1	1	1	1												
Cirsium palustre	1																					
Epilobium anagallidifolium	1	1	1		x	1	1	1	1	2												
Euphrasia sp.		1																				
Fragaria vesca							1															
Montia sp.					x																	
Parnassia palustris		1																				
Prunella vulgaris	1	1			1																	
Rumex acetosa			1				2															
Sagina procumbens				1			1	1														
Selaginella selaginoides	1	1					1															
Triglochin palustris										1												
Veronica serpyllifolia			1							1												
Viola riviniana		2		1																		
Acrocladium cordifolium			1																			
Brachythecium rivulare					1																	
Ctenidium molluscum	2																					
Cratoneuron commutatum		1																				
Drepanocladus aduncus					2																	
Fissidens adianthoides	1				1																	
Mnium undulatum	1		1	1																		
Thamnium alopecurum			1	1				1														
Nardus stricta	2	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		[illegible]													
Equisetum palustre	1	1		1		2			2		1		1		2							
Galium palustre	1	2	1	1	2		1	2	2	1			1									
Leontodon autumnalis	1	2				3					2											
Ranunculus acris											1											
R.flammula	2				1									1								
Trifolium repens	2			2	1		2	2	3			1										
Viola palustris	1		1	2	1							2										
Acrocladium cuspidatum	2	2	2		1	3	2	3	3		3	2	1	2								
Bryum pseudotriquetrum	2	1	1			3	2	3		2			1									
Hylocomium splendens		1		3		3					3		1									
Mnium hornum															1							
M.pseudopunctatum													1									
M.punctatum	2	1	3	2	1	5	5	4	2		4											
Philonotis fontana	2	1	1		2	3				1	2											
Aneura pinguis	2		1		1	1	1				1				1							
Pellia spp.			1				1						2	2								
D) CALCIFUGE SPECIES																						
Deschampsia flexuosa																1	1	x		2	1	
Eriophorum vaginatum													1	2		5	4	4				4
Calluna vulgaris																				x		
Galium saxatile				2			1							1			1	1	1			4
Aulacomnium palustre													1	3	5	2	1		1	x		
Dicranum scoparium																2						
Plagiothecium undulatum																		3	3		2	
Polytrichum commune									1			1	4	2	2	3	3	3	4	4	4	5
Sphagnum cuspidatum															1							
S.recurvum																			5		5	4
Splachnum ovatum																	x					
Calypogeia trichomanis													3	1	2	2	2	1	2	1	2	1
Lophozia ventricosa																		x	1			
Ptilidium ciliare																	1		1	1		1

existence to heavy sheep-grazing, it would seem to be the usual vegetation under lighter grazing of the intermediate zone between flushes and blanket bog.

The 7 constants comprise Festuca rubra, Acrocladium cuspidatum and Mnium punctatum, which are characteristic, and Anthoxanthum odoratum, Carex nigra, Festuca ovina and Nardus stricta. There are 10 near-constants, Eriophorum angustifolium, Epilobium anagallidifolium, Galium palustre, Bryum pseudotriquetrum, Philonotis fontana, Aneura pinguis, Equisetum palustre, Trifolium repens and Lophocolea bidentata, all but the last three being characteristic. Equisetum palustre and Trifolium repens are also near-constants in the species-rich gley nodum. In addition there are many characteristic species of lesser frequency, such as Carex curta, C. echinata, Parnassia palustris, Sagina procumbens, Onochophorus virens and Scapania irrigua. Thus this nodum is sharply distinguished from the other Juncus squarrosus noda at Moor House.

Juncus squarrosus communities elsewhere in Britain, and their relation to the noda established at Moor House

Whilst the literature contains many plant lists in which Juncus squarrosus occurs, much of this information is of little use to phytosociological studies. Very often only the more obvious species have been noted, under-recording the mosses, and sometimes neglecting the liverworts altogether.

However, two valuable works, 'Plant Communities of the Scottish Highlands' by McVean and Ratcliffe (1962) and 'The Vegetation of the Carneddau, North Wales. I Grasslands, Heaths and Bogs' by Ratcliffe (1959), give full species lists for quadrats of known size, allowing comparisons with the Moor House noda. Parallels can be found in these lists with each nodum, but there are also other communities containing Juncus squarrosus not found in the Moor House area, and they will be described after the parallels have been discussed.

In some instances the noda chosen by McVean and Ratcliffe for their Nardus - Juncus communities are rather different to those at Moor House, but examination of the individual lists shows that some are similar and the removal of the remainder to other noda often gives a close parallel.

The Podsol nodum (Table 6.11)

9 quadrat lists from the Scottish Highlands, 2 from the Carnedds, and 2 general lists from Cader Idris (Price Evans - 1932) and the Kelso area (Ragg - 1960) are given in the table. The Scottish lists are those given (omitting one) for the species-poor facies of Juncus squarrosus sub-alpinum which McVean and Ratcliffe make into an association. The soils are said to be 'gley podsols' (= peaty gleys) and shallow blanket peats, but are described as being not so waterlogged as the stands of Juncus squarrosus bog. The area covered by Juncus

The Juncus squarrosus communities on podsols.
(x = present; and in the Moor House lists only f = present in 50 - 80% of quadrats, c = present in over 80%; the Carneddau lists give average cover in 40 1/16 m² quadrats).

Place	MH	Scottish Highlands									Carneddau		Cader Idris	Kelso
Nodum	pod.	species-poor facies of Js sub-alpinum												
		1	2	3	4	5	6	7	8	9	1	2	1	1
Altitude (feet)		2475	2575	2450	2000	2100	1750	1650	1800	2700	1850	1750	1500-1800	
Aspect and Slope (degrees)		4 S	2 S	8 S	10 N	3 SE	3 SE	3 SE	3 S	33 S	20 W	20 SW		
Agrostis canina	x	1	2	3	4		3	3	3	5	3	2	x	x
A. tenuis	x	3			4					5	4	4	x	x
Anthoxanthum odoratum		3		4	3	2	4	1	3	4	4	3	x	x
Carex bigelowii	x	2	3		3					4				
C. binervis									+				x	
C. nigra	x											1	x	
C. panicea				2									x	
C. pilulifera								2						
Deschampsia flexuosa	c	3	2	2	3	2		3	3	3	2	1	x	
Eriophorum angustifolium									2					
Festuca ovina	c	4	4	5	3	8	3	5	3	3	7	7	x	x
Juncus squarrosus	c	9	9	9	7	6	7	6	7	7	5	4	x	
Luzula campestris	x					3	2		2		1	2	x	
L. sylvatica											1			
Nardus stricta	x	2	4		3	1	5	6	7	7	5	4	x	x
Poa pratensis														x
Sieglingia decumbens											1	1	x	
Calluna vulgaris														x
Cirsium palustre													x	
Dryopteris austriaca														x
Empetrum nigrum													x	
Erica tetralix													x	
Galium saxatile	c	5	3	4	5	4	3	3	5	3	4	5	x	x
Lycopodium sp.													x	
Oxalis acetosella														x
Polygala serpyllifolia													x	
Potentilla erecta	x			3	4			1	3		1	3	x	x
Rumex acetosella					3							1		
Vaccinium myrtillus	c	3	3	2		1		1		3	1	1	x	x
V. vitis-idaea	x								1					
Dicranum scoparium	x	1								2	1	2		
Hylocomium splendens	x	2	1		5				2	4	3	2		x
Hypnum cupressiforme	f										1	1		x
Plagiothecium undulatum	x				3				2	3				x
Pleurozium schreberi	c	4	5	1	3	1		1	3	2	3	3	x	x
Polytrichum alpinum	x									3				
P. commune	c	1	4	1	3						2	3	x	
Pseudoscleropodium purum													x	x
Rhacomitrium lanuginosum	x	1											x	
Rhytidiadelphus loreus	x					4				2	1	1		
R. squarrosus	c	2	4	4	4	3	2	5	3	4	4	2		x
Sphagnum papillosum											1		x	
S. recurvum											1			
Thuidium tamariscinum												1		
Lophocolea bidentata	c	1					3	1	3		1			
Lophozia floerkii	c	1	1						3	1				
Ptilidium ciliare	c	3	2	2					3		1	1		x
Cladonia pyxidata	x	1											x	
C. sylvatica	x	1												
C. uncialis	x												x	

squarrosus sub-alpinum is considerable, especially in the central Highlands. The other 4 lists are from podsols.

Comparison of Tables 6.2 and 6.11 shows some important differences between the noda, but examination of other lists shows that this is the best fit possible. Of the 49 species, 28 occur in the Moor House podsol nodum. Agrostis canina and Anthoxanthum odoratum are constants in Table 6.11, but very scarce and absent respectively in Table 6.2 - perhaps this is an indication that they have been grazed out of the Moor House podsols. Nardus stricta is a constant in Table 6.11 and there is a greater variety of herbs, though this is due to the general lists in which they may have been over-recorded.

In the mosses Hypnum cupressiforme is surprisingly absent from the Scottish lists, and Polytrichum commune scarce, but both are present in the Carnedds. Liverworts have much less cover in Table 6.11, and the three Moor House constants are the only ones that remain.

However, 5 constants are common to both tables - Deschampsia flexuosa, Festuca ovina, Galium saxatile, Rhytidiadelphus squarrosus and Pleurozium schreberi, which is a characteristic of the Moor House podsol nodum. Vaccinium myrtillus, a characteristic near-constant at Moor House is also well-represented. To sum up, it seems that the Scottish form of the Moor House nodum has a denser growth of grass, in which broad-leaved species are prominent, but bryophytes, especially liverworts, have less cover.

The Peaty Gley nodum (Table 6.12)

6 of the 8 Carneddau lists in the table are from peaty gleys; one is from a peaty podsol, and the other, and the two Scottish lists, are from bog. Unfortunately, McVean and Ratcliffe give only 4 lists for Juncus squarrosus bog, 2 of which show signs of flushing and are dealt with later, so it is impossible to determine how widespread the Moor House peaty gley nodum is in the Highlands.

Ratcliffe (1959) gives a vegetation map of the Carneddau, which shows that the Festuca-Nardus-Juncus communities, which compare with the podsol and peaty gley noda at Moor House, cover large areas, and probably similar vegetation is very extensive in the other Welsh mountains, the Pennines and the Southern Uplands.

Similar differences exist between Tables 6.3 and 6.12 as between 6.2 and 6.11 (the podsols). The Welsh communities are richer in broad-leaved grasses, Agrostis canina and tenuis being constants, but liverworts are again scarce. Calypogeia trichomanis, a characteristic constant at Moor House, is completely absent. Galium saxatile, Hylocomium splendens and Pleurozium schreberi are constants in Table 6.12, but are infrequent in the Moor House nodum, and Nardus stricta and

Juncus squarrosus communities in North Wales and the Scottish Highlands on wet peat and peaty gleys. (Moor House symbols as in Table 6.11).

Place	MH	Scot.H.		Carneddau in North Wales							
Noda	peaty gley	Js bog.		Festuca - Nardus- Juncus squarrosus				Festuca- J.squarrosus			Blkt. bog
		1	2	1	2	3	4	1	2	3	1
Altitude (feet)		2250	2650	1850	1650	1700	2150	3000	1900	1650	2275
Aspect and Slope (degrees)		25 S	-	15 N	10 NW	12 N	10 E	2	12 N	5 W	2
Agrostis canina	x	3		4	2	4	3	2	3	2	
A. tenuis	x			4	4	3	3	4	1	1	3
Anthoxanthum odoratum	x			2			5	1	1	4	
Carex bigelowii	x	3						1			
C. nigra	f		3		1	1			2	1	1
C. panicea				1	1	2					
Deschampsia flexuosa	f	2		1	2	4	2	4	4	4	2
Eriophorum angustifolium	x										1
E. vaginatum	x			1	2	1					4
Festuca ovina	c			7	7	7	5	6	5	5	2
Juncus squarrosus	c	8	8	5	5	5	5	6	8	8	8
Luzula campestris	x			1	2					1	
Molinia caerulea					1	1				3	
Nardus stricta	x		1	4	5	5	5		1	1	
Sieglingia decumbens				1							
Trichophorum cespitosum				1	1						
Armeria maritima		4									
Erica tetralix											4
Galium saxatile	x	3	3	4	5	4	5	5	3	4	2
Potentilla erecta	x	2	3	2	1				1	1	
Rumex acetosella								1			
Vaccinium myrtillus	x		2	3	3	2		1	1		5
Aulacomnium palustre	x	3	3					1			2
Dicranum scoparium	x		1	1	1			1		1	1
Hylocomium splendens			6	3	1	2	2	2	1	1	
Hypnum cupressiforme	x			1	1		1	1	1	1	1
Plagiothecium undulatum	f			1			1		3	2	4
Pleurozium schreberi	x	1		3	2	2	2	2	2	1	1
Polytrichum alpestre		2									
P. commune	c		2	5	4	4	4	4	5	4	3
Rhacomitrium lanuginosum		3						1			
Rhytidiadelphus loreus	x	3	4	1	1	3		4	2		3
R. squarrosus	x			1	2	1	4	3	2	2	
Sphagnum cuspidatum	x	2									1
S. papillosum		4									
S. plumulosum	x	4	2	1							4
Thuidium tamariscinum		1		1					1		
Diplophyllum albicans	x	4						1			
Leptoscyphus taylori		4									
Lophocolea bidentata	f			2	1	2		1	2		1
Lophozia floerkii	x			1				2	1		
Ptilidium ciliare	f	2	1	1		1	1				
Scapania gracilis		3									
Cetraria islandica	x	1	1								
Cladonia subsquamosa			1								
C. uncialis		2	+					1			

Vaccinium myrtillus are also more abundant in Table 6.12 than at Moor House.

However, Festuca ovina and Polytrichum commune are common constants to the two tables, and the near-constants of Table 6.3 - Carex nigra, Deschampsia flexuosa, Plagiothecium undulatum, Lophocolea bidentata, and Ptilidium ciliare are all well-represented in Table 6.12, Deschampsia flexuosa being a constant. There is a similar increase of hydrophilic species between Tables 6.11 and 6.12, as between 6.2 and 6.3. Carex nigra, Eriophorum vaginatum, Aulacomnium palustre, Polytrichum commune, Rhytidiadelphus loreus, Sphagnum cuspidatum and S. plumulosum have either a greater abundance, or appear in Table 6.12, and other plants of wet places, Trichophorum caespitosum, Diplophyllum albicans and Leptoscyphus taylori are present.

Table 6.12 contains 46 species, 30 of which occur in the Moor House nodum. But despite this similarity in overall composition, and the occurrence in both of species typical of very wet acid conditions, the balance of species shifts markedly as the broad-leaved grasses and the mosses of rather less-acid conditions are more abundant elsewhere than at Moor House.

A parallel to the peaty gley nodum occurring at Moor House where the dominance of Calluna in blanket bog has been affected by man's activities, is probably the Juncus squarrosus sub-association which Moore (1962) has created from some lists of

Calluna - Eriophorum - Sphagnum blanket bog in the Wicklow mountains. Deschampsia flexuosa, Plagiothecium undulatum and Calypogeia trichomanis are the three differential species of the sub-association, in which Calluna vulgaris, Eriophorum angustifolium and E. vaginatum are still prominent.

At lower levels in warmer conditions, Molinia caerulea is often the dominant plant on peaty gleys, but is rare in the North Pennines. Neither is it common in N. Wales, but in S. Wales it covers about half of the large area of rough grazings (Stapledon, 1936). Juncus squarrosus frequently accompanies it here, and one stand on Llangynidr Mountain, Brecon had 35% Juncus squarrosus, 15% Molinia, 15% Nardus and 5% Festuca ovina. Agrostis canina, Deschampsia flexuosa, Trichophorum caespitosum, Eriophorum vaginatum, Vaccinium myrtillus, Galium saxatile and Potentilla erecta were subsidiary species.

The Species-poor Gley nodum. (Table 6.13)

Only 4 lists were found comparable with the Moor House nodum, possibly because stands with Nardus and Juncus co-dominant have been avoided. The 3 Scottish lists come from the 14 given for the species-poor facies of Nardetum sub-alpinum. Only 7 of these contain Juncus squarrosus and 4 were omitted as they are more species-rich than the Moor House nodum - 2 of these appear in Table 6.14 (gley) and 2 in Table 6.16 (flush).

Selected lists from the species-poor facies of Nardetum subalpinum in the Scottish Highlands and one of Festuca-Nardus from the Carnedds compared with the species-poor gley nodum at Moor House.

	MH gley	Scottish H. 1	2	3	Carneddau
Altitude (feet)		2000	1300	1850	1750
Aspect and Slope (degrees)		3 SE	3 NW	3 SE	25 S
Agrostis canina	x	3			3
A. tenuis	c	2	2	3	3
Anthoxanthum odoratum	x	4	3	3	1
Carex binervis			2	2	1
C. nigra	x				1
C. panicea		1	4		1
C. pilulifera		1	3	2	1
Deschampsia cespitosa	x	1		1	
D. flexuosa	x		1		2
Festuca ovina	c	7	4	3	7
Juncus squarrosus	c	4	2	4	3
Luzula campestris	c	2	2	2	2
Nardus stricta	c	9	7	8	7
Sieglingia decumbens					1
Anemone nemerosa			1		
Galium saxatile	c	4	3	3	4
Pedicularis sylvatica			1		
Polygala serpyllifolia			2		
Potentilla erecta	x	3	3	3	3
Rumex acetosa (-ella?)	x		1		
Vaccinium myrtillus		1	3	5	4
Viola palustris	x			1	
V. riviniana			2		
Dicranum scoparium	x				2
Hylocomium splendens	x		2	3	2
Hypnum cupressiforme	c				1
Mnium cf. stellare			2		
Pleurozium schreberi	x	6	4	3	3
Polytrichum alpinum		1			
P. commune	x		1		1
Rhytidiadelphus squarrosus	c	6	1	3	2
Lophozia floerkii	x				1
Ptilidium ciliare	x			1	1
Cladonia sylvatica					1

Other lists in the 14 have few species, but even so McVean and Ratcliffe have set up a more species-rich nodum than that found along the streams at Moor House. The soils are said to vary from gleys with no H layer to podsols, but profiles of the selected sites are not available. The Carneddau soil type is a peaty gley, but the list fits better here than in the peaty gley nodum.

Of the 8 constants at Moor House (Table 6.6), Agrostis tenuis, Festuca ovina, Luzula campestris, Nardus stricta, Galium saxatile and Rhytidiadelphus squarrosus are present in each list, but Hypnum cupressiforme and Lophocolea bidentata are absent. As in the Moor House nodum, Deschampsia flexuosa, Polytrichum commune, Lophozia floerkii and Ptilidium ciliare have little cover, whilst selective species such as Deschampsia caespitosa and Viola palustris occur in both. The chief difference to the Moor House nodum is that Anthoxanthum odoratum, Carex pilulifera and Pleurozium schreberi have more cover, and they are constant species in the Scottish species-poor facies of Nardetum sub-alpinum.

Almost two-thirds of the species in Table 6.13 occur in the Moor House nodum, and as the constants are similar, it seems there is a good parallel between the nodum and these lists.

The gley species-rich nodum (Table 6.14)

The only parallel found to the Moor House nodum is Nardetum sub-alpinum in the Scottish Highlands. 1 of the 8 lists for the species-rich facies was excluded from the table as it contained some peat-loving species such as Molinia caerulea, but 2 lists were included from the species-poor facies, having been rejected from Table 6.13.

The Scottish nodum is richer floristically than the Moor House, having 122 species compared to 88, but there are 59 species common to both, and the Moor House stands are clearly much richer than the species-poor facies in Scotland. In comparing the individual quadrat data, it must be remembered that larger quadrats have more species, and the 31 quadrats of $1/4m.^2$ at Moor House do not cover as great an area as the 9 quadrats of $4m.^2$ in the Highlands. However, the 3 $4m.^2$ quadrats at Moor House (Table 6.8) have an average of 42 species, in comparison with the average of 43 in the species-rich facies of Nardetum sub-alpinum.

Of the 9 constants in the species-rich gley nodum at Moor House, 7; Agrostis tenuis, Anthoxanthum odoratum, Festuca ovina, Nardus stricta, Galium saxatile, Potentilla erecta and Rhytidiadelphus squarrosus are constants in Table 6.14, whilst Luzula campestris is a near-constant, and Lophocolea bidentata frequent, being the most abundant of the liverworts. The other

Table 6.14.

The species-rich facies of Nardetum strictae sub-alpinum in the Scottish Highlands, and a comparison with the species-rich gley and the flush noda at Moor House. (x = present, f = present in 50 - 80% of the quadrats, c = constant i.e. present in at least 80% of the quadrats).

Noda	Juncus squarrosus MH gley	Juncus squarrosus MH flush	Nardetum strictae sub-alpinum spp.-poor 1	spp.-poor 2	species-rich 1	species-rich 2	species-rich 3	species-rich 4	species-rich 5	species-rich 6	species-rich 7
Altitude (feet)			2200	1450	1500	2300	1750	1250	1600	1250	1500
Aspect and Slope (degrees)			2 SE	5 SW	20 N	30 NE	5 W	28 W	20 SW	40 NE	5 E
Agrostis canina	x	x		6	5	3	3	4	3	4	
A.stolonifera		x	2						3		3
A.tenuis	c	c	1	6	5	2	3	4	2	3	3
Anthoxanthum odoratum	c	c	4	5	5	3	4	4		3	5
Arrhenatherium elatius										3	
Briza media		x						1		1	
Carex binervis			2	2		2			2		
C.demissa	x	x				2	3				
C.echinata		x				2	3	4	3	4	4
C.flacca	x	x								3	2
C.hostiana					2						
C.nigra	x	c							2		3
C.panicea	x	x	2	3	4		4	4	3	3	3
C.pilulifera			2	2							
C.pulicaris	x	x			4	3	3	3		4	2
Deschampsia cespitosa	x	x	1	2		3	3			2	
Eriophorum angustifolium		f				2		2	4		1
Festuca ovina	c	c	3	4	3	5	3	4	3	3	4
F.rubra	x	c		2	4	3		2			
Holcus lanatus	x	x						3	2	4	4
Juncus acutiflorus								2			
J.effusus	x	x		2							
J.kochii		(x)					2		3		1
J.squarrosus	c	c	1	3	3	2	5	3	7	2	3
Luzula campestris	x	x	2		3	3	1	3	1		3
L.sylvatica										2	
Molinia caerulea								1			
Nardus stricta	c	c	8	8	7	7	7	8	7	5	8
Sieglingia decumbens	x			3							
Trichophorum cespitosum									2		
Achillea millefolium	x			2							
A.ptarmica	x							2			2
Alchemilla alpina						3				2	
A.filicaulis											3
A.glabra		(x)			3		3				
A.vestita		(x)				3	3				
A.wichurae						4					
A.xanthochlora										2	
Anemone nemorosa			2								
Angelica sylvestris				1							
Calluna vulgaris										2	
Caltha palustris		x								1	1
Campanula rotundifolia			3		2	3		2			
Cardamine flexuosa										1	
Cerastium holosteoides	x	x			2	1	2	1			
Cirsium heterophyllum										5	
C.palustre								2			
Crepis paludosa					2						
Empetrum hermaphroditum						3					
Epilobium anagallidifolium	x	f					2				
Equisetum palustre	f	f				2		2			
Euphrasia sp.	x	x			3	2	3		2		1
Filipendula ulmaria					2						
Galium boreale						1					
G.saxatile	c	x	3	3	2	2	1	2		2	1
G.verum										3	
Geranium sylvaticum						1					
Geum rivale		(x)				2					
Hypericum pulchrum										3	
Lathyrus montanus										1	
										2	

Noda	MH gley	MH flush	1	2	1	2	3	4	5	6	7
Leontodon autumnalis	x	x		2	3		3	+	3		3
Linum catharticum					1					2	
Lysimachia nemoreum										3	
Oxalis acetosella			1		1						
Plantago lanceolata	x	x		2	3			2			
Polygonum viviparum				3	1	3	3				
Potentilla erecta	c	x	3	4		2	3	3	3	3	3
Prunella vulgaris	x	x			+		+			3	
Ranunculus acris	x		1	2	3	2	+	3		3	3
R.flammula	x						2				
Selaginella selaginoides	x	x				3					
Senecio jacobea											2
Silene acaulis						1					
Succisa pratensis								2		3	3
Taraxacum officinale	x	x			3		2	1			3
Thalictrum alpinum					3	2	+				
Thymus drucei	x		3			3					
Trifolium repens	f	f	2	1			3	3		1	
Vaccinium myrtillus			3			2					
Veronica chamaedrys	x									2	
V.officinalis	x							2			
Viola sepium					2						
Viola palustris	x	x	3				2		3		
V.riviniana	x	x		4	3	3		2			3
Acrocladium cuspidatum	x	c			2		3			2	3
A.stramineum	(x)	x							2		
Atrichum undulatum	x			1			1			1	
Aulacomnium palustre	x								1		
Brachythecium rivulare		x			2						
Bryum pseudotriquetrum		f					1				
Climacium dendroides	x						2			2	1
Ctenidium molluscum	x	x					1				
Dicranum bonjeani										1	
Hylocomium splendens	f	x	5	1	4	4	2	3	1	3	2
Mnium hornum	x	x						1			
M.pseudopunctatum	x							2	2		2
M.punctatum	x	x			2		3				
M.undulatum	x	x		1	3			2		1	
Philonotis fontana		f					2				
Pleurozium schreberi	x					2					
Polytrichum alpinum	x		1	3		2					
Pseudoscleropodium purum	x		1	1	3	2		3			2
Ptilium crista-castrensis					1						
Rhacomitrium lanuginosum						1					
Rhytidiadelphus loreus						2					
R.squarrosus	x	x	1	3	4		2	3	3	2	3
R.triquetrus	x	(x)	1			3					
Sphagnum plumulosum	x	x				3					
S.recurvum									4		
S.squarrosum									1		
S.subsecundum									1		
S.warnstorfianum						2			3		
Thuidium tamariscinum	x	(x)			3	3		4	2		1
Aneura cf. sinuata							1		2		1
Chiloscyphus polyanthus											2
Lophocolea bidentata	c	c		2	2			2	2	1	3
Lophozia lycopodioides						2					
L.quinquedentata		x				2					
Pellia fabbroniana		x					1		2	1	1
Ptilidium ciliare	x					1					
Scapania dentata							1				
S.irrigua		x							3		

constants in the 9 Scottish lists, Agrostis canina, Carex panicea and Hylocomium splendens, are present at Moor House, Hylocomium being a near-constant. 2 of the other near-constants at Moor House, Equisetum palustre and Trifolium repens, occur in the Scottish nodum, but Hypnum cupressiforme is strangely absent.

Mildly calcicolous herbs and sedges are even better-represented in the Scottish nodum to the Moor House. Acid-peat loving species, such as Deschampsia flexuosa and Polytrichum commune are absent from both. Several of the more hydrophilic species found only in the flushed-peat nodum at Moor House are present in Table 6.14 and there are in fact 59 species in common between the two noda, but a comparison of the constants makes it clear that the species-rich Nardetum is much more closely related to the species-rich gley than the flushed peat nodum at Moor House.

The soil conditions described for the Scottish nodum - gleys on slopes with calcareous irrigation - are identical to those obtaining at Moor House. The soils have a much greater Ca^{++} content than those of the species-poor communities, but are not significantly different in K^+ or P_2O_5. Thus, contrary to the statement of McVean and Ratcliffe (p.59), species-rich Nardetum sub-alpinum does occur outside the Central Highlands.

Table 6.15.

The three lists for the species-rich facies of <u>Juncetum squarrosi sub-alpinum</u> in the Scottish Highlands, and a comparison with the Moor House flush and species-rich gley noda.

Noda	MH gley	MH fl.	spp-rich Jsq. 1	spp-rich Jsq. 2	spp-rich Jsq. 3
Altitude (feet)			2250	2000	2200
Aspect a nd Slope (degrees)			10 N	10 N	10 NE
Agrostis canina	x	x	3	3	3
A. tenuis	c	x	3		
Anthoxanthum odoratum	c	c	3	3	3
Carex demissa	x	x			2
C. echinata		x	2	3	3
C. hostiana					2
C. nigra	x	c	1	4	
C. panicea	x	x	3	4	4
C. pulicaris	x	x	2	3	1
Eriophorum angustifolium		f			2
Festuca ovina	c	c	4	4	4
Holcus lanatus	x	(x)		3	
Juncus acutiflorus				3	
J. effusus		x	3		
J. kochii		x	+		2
J. squarrosus	c	c	8	7	7
Luzula campestris	c	x	+		1
Nardus stricta	c	c	4	4	6
Alchemilla glabra		(x)	3	4	2
Cerastium holosteoides	x	x	2	2	
Crepis paludosa				3	
Epilobium anagallidifolium	f	f	2	1	
Equisetum sylvaticum					1
Erica tetralix					2
Euphrasia sp.	x	x		3	2
Galium saxatile	c	x	+		
Geum rivale		(x)		3	
Leontodon autumnalis	x	x	2	3	3
Linum catharticum			2		2
Lysimachia nemoreum					2
Narthecium ossifragum				1	2
Parnassia palustris		x		3	
Pinguicula vulgaris			2		2
Polygonum viviparum			3	3	2
Potentilla erecta	c	x	3	3	3
Prunella vulgaris	x	x		3	1
Ranunculus acris	x		1	3	

	g	f	1	2	3
Rhinanthus minor agg.				2	
Selaginella selaginoides	x	x	1	2	2
Taraxacum officinale	x	(x)		1	1
Thalictrum alpinum			3	3	3
Trifolium repens	f	f	3		
Vicia sepium				2	
Viola palustris	x	x	1		3
V. riviniana	x	x		3	
Acrocladium cuspidatum	x	c	4		3
Aulacomnium palustre	x		2		3
Brachythecium rivulare		x	3		
Bryum pseudotriquetrum		f	2	2	1
Campylium stellatum		(x)	1		3
Drepanocladus revolvens		x			2
Hylocomium spendens	f	x	3	5	3
Mnium pseudopunctatum	x		4		3
M. punctatum	x	c		4	
M. seligeri			2	1	
M. undulatum	x	x	3	2	3
Philonotis fontana		f	4	2	4
Rhytidiadelphus squarrosus	c	x	2	3	+
R. triquetrus	x	(x)	1	3	
Sphagnum plumulosum	x	x	+		3
S. subsecundum					2
S. warnstofianum			+		4
Thuidium tamariscinum	x	(x)	2		
Aneura pinguis		f	2	1	
A. cf. sinuata			1		2
Calypogeia trichomanis	x				2
Chiloscyphus pallescens					2
C. polyanthus				2	
Lophocolea bidentata	c	c	2	3	
Pellia fabbroniana		x	3		3
Scapania dentata				2	
S. irrigua		x			3
S. nemerosa				1	

The Flushed-peat nodum (Tables 6.15 and 6.16)

23 lists from 9 of the Scottish Highland noda have been collected together in the 2 tables. No other lists comparable to the Moor House flushed-peat nodum were found in the literature. Juncus squarrosus is the dominant of 4 lists and 3 of them, those forming the species-rich facies of Juncus squarrosus sub-alpinum have been placed in Table 6.15. The other, of Juncus squarrosus bog, is intermediate between these and the peaty gley lists, and has been placed at the acidic end of the ecocline in Table 6.16. In the other stands contained in the table Juncus squarrosus has a small cover value, being just a community member. If the 3 lists in Table 6.15 were placed in Table 6.16, they would come in the middle of the ecocline, indicating that at least up to this point Juncus squarrosus can dominate flushed-peat communities if competition from other species is reduced, for example by sheep-grazing.

The 3 lists compare well with the Moor House flushed-peat nodum in Table 6.9. All the Moor House constants and near-constants are present except Festuca rubra, and 9 of these are characteristic of the nodum. 72 species occur in Table 6.15 and 46 of them are found in the flushed-peat nodum. A further 5 species occur in the species-rich gley nodum at Moor House, but 15 of the 46 are absent from this, indicating clearly to which nodum the three lists belong. 3 lists are hardly

Transition from species-rich to poor in the flushed-peat communities containing Juncus squarrosus in the Scottish Highlands. (Lists from Ratcliffe and Mc.Vean, sorted and reanalysed). MH column indicates species present in the equivalent gradient at Moor House, (Table 6.10):- (x) = species present only in the large quadrats, where x is followed by a letter this indicates the group in which the species occurs at Moor House in the instances where this is different.

Noda		Carex-Sax.ais	Hypno-Caricetum alpinum						J.acutifl-Acroclad. cuspidatum		Na.sub-alpinum spp rich	species poor		Sphagno - Caricetum sub-alpinum						alpinum	Js bog
	MH	1	1	2	3	4	5	6	1	2	1	1	2	1	2	3	4	5	6	1	1
Altitude (feet)		1900	2250	1800	2000	2000	1700	1000	750	1200	1700	1200	1600	2150	1000	1750	2000	1750	730	2650	2500
Aspect and Slope (degrees)		-	12 N	25 NW	20 NE	7 W	25 N	5 W	3	25 S	20 E	15 S	30 N	2	-	3	12 S	-	-	10 NE	25 S
A) OVERALL SPECIES (= a + c at MH)																					
Agrostis canina	x	3	2					1			2	2	5			3				3	
A.stolonifera	x														5				3		
A.tenuis	x						+	3	2		4	4	5				2				3
Anthoxanthum odoratum	x			2	2		4		3		3	3	3			3	3	3			
Carex binervis			4										4								
C.curta	x													+						2	
C.demissa	x	2	4		+										2						
C.echinata	x			+	5	5	4	5	2	5	3			5	6	5	8	5	4	6	3
C.nigra	x		3	5	4	8	7	5		2	3			5	6	7	3	5	8		
C.panicea	x	5	4	4	4	3	3	3	4	4	4	3			2	3		2			
C.pilulifera												2	3								
C.vaginata																					1
Deschampsia cespitosa	x	+		2									4								
Eriophorum angustifolium	x		4		3	3	3	2	2					2	5		3	3	3	3	3
Festuca ovina	x	3	1	3	2		5	2	2		3	3	5			3	2		3		3
Holcus lanatus	(x)				2			3	3	3	2	3							2		
Juncus acutiflorus						2	1		6	9											
J.articulatus	x			3	6			3							2						
J.effusus	x							2													
J.kochii	x		3		4		3		3						3					2	
J.squarrosus	x	1	4	3	3	1	3	2	2	1	3	6	3	3	2	3	3	3	2	1	8
Luzula campestris	x			3	1	2		2	1		2	2	3	+		1		2		2	
L.sylvatica													2								
Molinia caerulea							2	4	4		5	3			4			2			
Nardus stricta	x	1	5	3	3	2	4	2	3	3	8	7	5		2		3	4	1	2	3
Sieglingia decumbens								2				3									
Trichophorum cespitosum		1	3								2	2	2				1				4
Betula sp.									1										1		
Blechnum spicant													2								
Calluna vulgaris		1										3									2
Drosera rotundifolia									1												
Empetrum hermaphroditum			2	+																	2
E.nigrum	(x)						2														
Equisetum palustre	x			2							1										
Erica tetralix									2										5		
Euphrasia sp.	xb			1	3		3	3	2		3	2	1								2
Filipendula ulmaria						1															
Lathyrus montanus												1									
Lycopodium selago			2																		
Lysimachia nemoreum						3		3													
Narthecium ossifragum			3		3		1		3		2	1	1				2		3		3
Orchis ericetorum								2													
Oxalis acetosella													2								
Pedicularis sp.								1	2												
Pinguicula vulgaris		+	2	2	+		1				2					2				1	2
Potentilla erecta	x	2	3	3	2	2	4	4	4	3	3	4	2		2	3	4	2	3		4
Salix aurita							+		1		2										
Succisa pratensis			2		2			5	4		3	3							3		3
Thelypteris oreopteris										2											
Viola palustris	x							3		3	3			3	3			5		3	2
V.riviniana	xb	2										4	3								
Acrocladium sarmentosum									2											2	
Camptothecium nitens			3	5																	
Cinclidium stygium							1														
Dicranum scoparium	xd						2						1								
Drepanocladus exannulatus															3						
D.uncinatus				2																	
Hylocomium brevirostre							2														
H.splendens	x	1	3	3	4	+	4	4	2	2	3	4	5						3		4
Mnium hornum	x						1					2									
M.punctatum	x				3	1						2									
Pseudoscleropodium purum				2	3		2	1		1	3	3							1		
Ptilium crista-castrensis							3														
Rhytidiadelphus squarrosus	x		3	2	4	+	3	3	1	3	2	3	2				2				2
Sphagnum subsecundum								4	7				2		9		1		5	5	
Thuidium tamariscinum	(x)			2		5	2	2	1	1	1	2	5						2		
Aneura multifida									1												
A.pinguis	x						1		2												
Chiloscyphus polyanthus			2						1												
Lophocolea bidentata	x			1	1		2	1	+	1	2	2									
Lophozia quinquedentata	(x)		3																		
Marsupella emarginata		1																			
Scapania gracilis	x												2								
S.irrigua	x		1																		
S.nemerosa							1														
S.undulata		+												1							

Table 6.16 cont.

B)RICH-FLUSH SPECIES	MH	1	1	2	3	4	5	6	1	2	1	1	2	1	2	3	4	5	6	1	2
Briza media				3		3			3												
Carex aquatilis						8															
C.dioica	x		4		2		2									2					
C.pulicaris	x	2	5	4	4	2	4	2	2		1										
Festuca rubra	xc		1	2		2	3		3	2											
Phleum commutatum								2													
Achillea ptarmica	x								3	3											
Alchemilla filicaulis		2																			
A.glabra	(x)					4	2														
A.xanthochlora			2	3	2																
Anemone nemerosa			1																		
Caltha palustris	x			3	2	1															
Campanula rotundifolia		1	1																		
Cardamine pratensis	x			2		2															
Cerastium holosteoides	x			1		1															
Cirsium palustre	x									3											
Coeloglossum viride							1														
Crepis paludosa					3		4		4												
Epilobium anagallidifolium	x					1	2	2	2	+											
Galium boreale		1																			
Geum rivale	(x)			3			1														
Leontodon autumnalis	xc			+	4	2	3	3	2		3	1									
Linum catharticum			2	1			2		1												
Parnassia palustris	x				3		3														
Plantago lanceolata							2	3			4										
Polygonum viviparum		1	2	3	+	3	3				3										
Prunella vulgaris	x			3	3	2	2	1	1	2	2										
Ranunculus acris	xc			4	3	2	3	1	1	2	3	2									
R.flammula	xc		1		2			2	2	2											
Rhinanthus sp.					+		1	1			2										
Rumex acetosa	x			1		1															
Sagina procumbens	x					1															
Saxifraga aizoides		2		+																	
S.oppositifolia		5																			
Selaginella selaginoides	x	3	2	1	1	2	3	1			1										
Taraxacum officinale	(x)	2	2	+			3			1	1										
Thalictrum alpinum		5	4	4	4		3														
Thymus drucei		1	2																		
Tofieldia palustris		4																			
Trifolium repens				3	+	3			2		+										
Triglochin palustris	x				1	3															
Acrocladium cuspidatum	xc		2	3	5	3	3	2	2	3				1							
Blindia acuta		3																			
Brachythecium rivulare	x				3																
B.rutabulum										2											
Breutelia chrysocoma					2		3	2	3												
Bryum pseudotriquetrum	xc	3	4			3			2												
Campylium stellatum	(x)	2	3						2												
Climacium dendroides						3															
Cratoneuron commutatum	x					3															
Ctenidium molluscum	x	3	4		3	1		1													
Drepanocladus revolvens	(x)	5	3				1		1												
Fissidens adianthoides	x		1																		
F.osmundoides		1																			
Mnium pseudopunctatum	xc			1		2	1														
M.undulatum	x			2	2	3	1	1													
Philonotis fontana	xc		2	2	1	2															
Rhytidiadelphus triquetrus		1	2	1	4		3														
Sphagnum squarrosum										3											
S.warnstoffianum				2			4		7												
Thuidium delicatulum				1																	
Aneura sinuata			3				1														
Pellia sp.	xc				1	2			1	2											
D)CALCIFUGE SPECIES																					
Carex bigelowii																				1	
Deschampsia flexuosa	x											4		3							
Eriophorum vaginatum	x													4						4	1
Galium saxatile	x	1					3				2		3			2	3				
Polygala serpyllifolia											2	3				1			3		
Vaccinium myrtillus													2							1	
V.vitis-idaea													1								
Acrocladium stramineum	xa													2		1				1	
Aulacomnium palustre	x		1	2							1			1		3	1		5		3
Hypnum cupressiforme	xa												2								1
Plagiothecium undulatum	x												2								
Pleurozium schreberi												2	2								3
Polytrichum commune	x							1	2				2	4			3	5	2	2	2
Rhytidiadelphus loreus	x						3					2	4								3
Sphagnum lindbergii																				6	
S.palustre	xa										3							8			
S.papillosum														5	2	6	3			6	4
S.plumulosum	xa		3				3				2		3	3	3	6		4	5	5	7
S.recurvum	x													9	4	6	9	4		3	
Anastrepta orcadensis													1								
Calypogeia trichomanis	x		1				1				1	2				1			1		3
Diplophyllum albicans													2								
Lophozia ventricosa	x																	2			
Ptilidium ciliare	x												1							2	2

sufficient to show any special features the flushed-peat nodum may have in Scotland, but 2 species rare in N. England are prominent - Polygonum viviparum and Thalictrum alpinum.

Table 6.16 gives a better idea of the typical species of the flushes in which Juncus squarrosus occurs. Only 5 of the 72 species in Table 6.15 are absent. The Scottish ecocline is closely parallel to that at Moor House, allowing for the greater number of species present - the Moor House quadrats cover less than a fifth of the area of the Scottish. Table 6.10 continues the Moor House ecocline into the peaty gley nodum, but this was omitted from Table 6.16 to avoid complexity. Therefore, the overall category in this table corresponds to both the overall (i.e. extending to the peaty gley) and flush groups of species in Table 6.10.

Of the 76 species in the overall category, 30 are found in the corresponding groups at Moor House, and only 2 (Euphrasia sp. and Viola riviniana) in the rich flush group and 1 (Dicranum scoparium) in the calcifuge group. Constants or near-constants in the group number 12. Anthoxanthum odoratum, Carex nigra, Eriophorum angustifolium, Festuca ovina, Nardus stricta and Rhytidiadelphus squarrosus are constants or near-constants in the Moor House nodum, whilst Carex echinata, C. panicea, Luzula campestris, Potentilla erecta and Hylocomium splendens are present, only Narthecium ossifragum being lacking.

The rich-flush group of species is considerably larger in the Scottish ecocline, many species coming from the very rich Cariceto - Saxifragetum aizoidis and Hypno - Caricetum alpinum noda. There are 63 species, 24 being found in the rich-flush and 9 in the flush group at Moor House, but almost all the Moor House group of rich-flush species occur in the Scottish group. It is therefore not surprising that the Moor House and Scottish constants are different.

As at Moor House the calcifuge group of species is smaller in number with 24. 10, including Deschampsia flexuosa, Eriophorum vaginatum, Aulacomnium palustre, Plagiothecium undulatum, Polytrichum commune and Sphagnum recurvum are in common with the calcifuge group at Moor House, and 4 with the overall group.

It must be mentioned that Juncus squarrosus occurs less frequently in the noda at the basic end of the ecocline. There are 25 lists in the Cariceto - Saxifragetum aizoidis nodum, but Juncus squarrosus is only present in 2, whereas it is present in 6 out of the 9 lists forming the Sphagno - Caricetum sub-alpinum nodum.

Other Communities.

Juncus squarrosus in grasslands on brown earths (Table 6.17)

9 of the 20 lists in the species-poor Agrosto-Festucetum nodum of the Scottish Highlands contain Juncus squarrosus and

Table 6.17.

Lists containing Juncus squarrosus from the Species-poor Agrosto-Festucetum and Alchemilleto-Agrosto-Festucetum noda in the Scottish Highlands, in comparison with the species-rich gley nodum at Moor House, and a list for high-level grassland on Cader Idris. (x = present, o = constant).

Noda	MH gley	Cader Idris	species-poor Agrosto-Festucetum 1	2	3	4	5	6	7	8	9	Alch-Ag-Fest. 1	2
Altitude (feet)		1600-2900	2000	2500	1750	2000	1000	2100	2250	1000	1200	2400	1900
Aspect and Slope (degrees)			30 W	20 S	2	25 N	-	20 W	12 E	28 NW	-	30 NE	-
Agrostis canina	x		4	6	2	5	3	7	9	3	5	2	
A. tenuis	o	x	7	6	8	4	7	7	9	5	8	4	5
Anthoxanthum odoratum	c	x	4	5	4	5	3	3	4	5	3	3	4
Carex bigelowii			1	3									
C. binervis					2	1		2	2	3			
C. demissa	x				2								
C. echinata					3	2			2		2		
C. nigra	x									4	3		
C. panicea	x				3	2	3			3	2		
C. pilulifera		x		3	2	3	3	3		3	+	1	
C. pulicaris	x				2							2	
Deschampsia cespitosa	x		3			3		2	3			2	
D. flexuosa	x			3				1		5	+		
Eriophorum angustifolium				2					1				
Festuca ovina	o	x	4	5	4	5	5	5	5	5	4	5	5
F. rubra	x											3	1
Holcus lanatus	x						2						
Juncus effusus	x				1								
J. squarrosus	c	x	1	4	3	2	3	3	3	4	2	2	2
Luzula campestris	c	x		3	3	3	3	1	2	3	3	2	3
L. sylvatica			2					2		3			
Molinia caerulea							3						
Nardus stricta	c	x	2	5		4	3	4	3	3	2	3	2
Sieglingia decumbens	x						4						
Trichophorum cespitosum					2	3			2				
Achillea millefolium	x						3						4
A. ptarmica	x										2		
Alchemilla alpina			3									4	7
A. glabra													1
A. vestita												4	3
Blechnum spicant		x				2		1		2		2	
Calluna vulgaris													2
Campanula rotundifolia		x							2				
Cardamine flexuosa													1
Cerastium holosteoides	x						1						
Empetrum nigrum	(x)	x											
Euphrasia sp.	x							1			2		2
Galeopsis tetrahit		x											
Galium saxatile	o	x	3	5	2	4	3	4	3	3	3	3	2
Geum rivale												3	
Leontodon autumnalis	x	x	+		1	2			2				
Lycopodium spp.		x											
Orchis ericetorum			1								+		
Pedicularis sylvatica											1		
Plantago lanceolata	x				2						2		
Polygala serpyllifolia	x	x									2	1	
Polygonum viviparum								4				4	
Potentilla erecta	o	x	3	4	4	5	4	5	4	5	3	4	

	MH gley	Cader Idris	1	2	3	4	5	6	7	8	9	1	2
Prunella vulgaris	x											2	2
Ranunculus acris	x		+		3		2		2		2	2	2
R. flammula					1								
Rumex acetosa										1			
Selaginella selaginoides	x											2	1
Succisa pratensis					1		3				+		
Taraxacum officinale	x				1				3				2
Thalictrum alpinum												4	
Thymus drucei			2									5	5
Trifolium repens	x												4
Trollius europaeus												2	
Vaccinium myrtillus		x	2	3		2		3		3		3	
V. vitis-idaea		x											+
Viola riviniana	x	x	3	2	4	4	3	3	3		4	3	2
Campylopus fragilis												1	
Ctenidium molluscum	x											3	
Dicranum scoparium	x											2	
Hylocomium splendens	x		7	5	5	4	4	5	3	3	3	4	4
Hypnum cupressiforme	x			3	2		3						
Mnium hornum	x									3			
M. punctatum	x				1								1
M. undulatum	x												2
Plagiothecium undulatum				2		1				4			
Pleurozium schreberi	x					1		4		1			2
Pohlia nutans	x												1
Polytrichum alpinum	x							2					3
P. commune	x					2	3			3	1		
Pseudoscleropodium purum	x		3		4		4	3		2	2	3	
Rhacomitrium lanuginosum		x											
R. canescens													2
Rhodobryum roseum	x												1
Rhytidiadelphus loreus	x		3			1		3		2			
R. squarrosus	o		4	5	3	2	3	3	3	2	3	2	4
R. triquetrus	x		3									4	
Sphagnum plumulosum	x					2							
Thuidium delicatulum												4	
T. tamariscinum	x		3		2	3	3			3	3		4
Calypogeia trichomanis	x										1		
Frullania tamarisci												1	
Lophocolea bidentata	o				2		2				2		
Lophozia floerkii	x			2									
L. hatcheri													1
Cetraria islandica		x											
Cladonia sp.		x											
C. pyxidata												2	
Peltigera canina							1					1	

have been placed in the table, together with 2 from the slightly richer Alchemilleto - Agrosto - Festucetum. They are compared with a list for high-level grassland on Cader Idris (Price, Evans, 1932) and the species-rich gley nodum at Moor House.

Many of the species-poor Agrosto-Festucetum stands are on well-drained alluvium, especially in North and West Scotland where other suitable soils are rare, and most of the lists come from this area. As the soils become more waterlogged they grade into Nardetum sub-alpinum. The dryness of the soil suggests that the stands would resemble the Moor House podsol nodum, but this is not so, since the species requiring mor humus have little cover or are absent. But there is a considerable similarity between these lists and the Moor House species-rich gley nodum. 8 of the Moor House constants are also constant here, only Lophocolea bidentata having less cover, and this is correlated with the lower cover of Juncus squarrosus. Carex pilulifera, Viola riviniana and Hylocomium splendens are the other constants of the brown earth stands and only the Carex is absent at Moor House. Of the 93 species, 54 occur in the species-rich gley nodum at Moor House. Despite the similarity, it is doubtful if Juncus squarrosus could ever become dominant on such well-drained soils. If the grazing pressure were such that it favoured the spread of species unpalatable in summer, Nardus stricta would assume dominance.

Table 6.18.

Lists of the chionophilous noda of <u>Nardus stricta</u> which contain <u>Juncus squarrosus</u>.

Noda	Nardus-Trichophoretum			Trich-Ns	Nardus-Pleurozium		Vacc.-Ns
	1	2	3	1	1	2	1
Altitude (feet)	2000	2750	2200	2100	2800	2900	2600
Aspect and Slope (degrees)	5 NE	2 NW	2 N	2 E	5 S	7 NW	10 E
Agrostis canina						3	
A.tenuis			2	4	1		3
Carex bigelowii		1	2			3	3
C.panicea			1		2		
C.pilulifera					2		
Deschampsia cespitosa					5	3	
D.flexuosa		+	3	1	+	3	3
Festuca ovina					3	3	1
Juncus squarrosus	1	2	1	1	1	2	2
Molinia caerulea				2			
Nardus stricta	6	9	8	4	8	8	7
Trichophorum cespitosum	5	2	5	8			
Calluna vulgaris	2			3			
Chamaepericlymenum suecicum							1
Empetrum hermaphroditum	1	3	2	2		1	5
Euphrasia frigida			1			2	
Galium saxatile	+				1	3	2
Juniperus nana	1						
Leontodon autumnalis						1	
Lycopodium alpinum	3	+	3				+
L.selago	2		2	3			
Narthecium ossifragum	1		2	3			
Orchis ericetorum	2						
Potentilla erecta	3	3	3	5	3	3	2
Solidago virgaurea	2						
Succisa pratensis	2						
Vaccinium myrtillus	3	1	2	2	2	3	5
V.uliginosum	4	4	4				2
V.vitis-idaea						1	3
Viola palustris						3	
V.riviniana					2		
Dicranum scoparium			1			3	1
Hylocomium splendens					4	6	5
Hypnum cupressiforme		1	+			3	2
Plagiothecium undulatum						3	3
Pleurozium schreberi		1	+		1	3	3
Polytrichum alpinum						3	
P.commune				+			1
P.juniperinum			1				
Rhacomitrium lanuginosum	7	4	5	+	1	3	3
Rhytidiadelphus loreus		1	1		3	4	5
R.squarrosus					2		
Sphagnum plumulosum				2		4	2
Alicularia scalaris			1				
Anastrepta orcadensis			1			3	
Anastrophyllum donianum		4				2	1
Calypogeia trichomanis						2	
Diplophyllum albicans		1					
Leptoscyphus taylori		1					
Lophozia alpestris			1				
L.floerkii			1			1	
L.quinquedentata							1
L.ventricosa							2
Pleurozia purpurea			1				
Ptilidium ciliare	3				3	3	3
Scapania gracilis		3					
S.nimbosa						1	
Cetraria aculeata		1					
C.islandica	3	3	3	1		2	3
Cladonia bellidiflora		2	2				
C.gracilis		3					1
C.pyxidata		1	+				
C.rangiferina	2	1					
C.sylvatica	3			+		1	3
C.tenuis		1	3				
C.uncialis	3	2	3	2			1

Juncus squarrosus in chionophilous Nardeta (Table 6.18)

Long snow-lie, by reducing the growing season, by causing long-continued waterlogging and by giving a slight flushing effect during the melting period results in different combinations of species growing together and thus produces new noda.

Such communities are absent in England, but widespread in the Scottish Highlands, very often being dominated by Nardus stricta. Juncus squarrosus is frequently present and 7 lists from 4 different noda have been brought together in the table to illustrate this type of habitat. There is quite a variety of species, podsol-favouring such as Vaccinium myrtillus and vitis-idaea, wet peat plants such as Narthecium ossifragum, Calypogeia trichomanis and Leptoscyphus taylori, plants requiring some base such as Leontodon autumnalis and Viola spp. and oceanic species, such as Pleurozia purpurea and Scapania nimbosa.

Juncus squarrosus in ericoid heaths (Table 6.19)

7 rather varied lists are given in the table of selected heath stands in which Juncus squarrosus occurs. The species list is such that if Calluna vulgaris and the Erica spp. were removed by continued heavy grazing, a community containing species of the podsol nodum would remain.

Table 6.19.

Juncus squarrosus in ericoid heaths in Scotland and Wales.
(x = present, and d = dominant).

Place Nodum	Scot.High. Callunetum vulgaris	Carneddau, N.Wales Vaccinium heath		Calluna heath	Kelso heath	burned heath	Lammermuir moist Call. heath
Altitude (feet)	1700	1300	1500	1500	700 - 1200		700 - 1500
Aspect and Slope (degrees)	5 NW	32 N	33 SW	30 SW			
Agrostis canina			3	2			x
A. tenuis		4	4	1			x
Anthoxanthum odoratum				2			x
Carex binervis				1	x		
C. nigra					x		x
C. pilulifera			1		x	x	
Deschampsia flexuosa	2		4	3	x		x
Festuca ovina		6	4	1	x		x
Juncus squarrosus	1	4	1	1	x	x	x
Luzula campestris		2	1				x
L. sylvatica					x		
Molinia caerulea		1					x
Nardus stricta		4					x
Poa annua		1					
Trichophorum cespitosum							x
Calluna vulgaris	10		3	9	d	d	d
Empetrum nigrum		1					x
Erica cinerea	2		2	5			x
E. tetralix					x	x	
Galium saxatile		3	3	1	x		x
Genista anglica	2						
Listera cordata	2						
Polygala serpyllifolia		1	1	1			
Potentilla erecta	+	1		2	x		x
Rumex acetosella		1					
Trientalis europaea	1						
Vaccinium myrtillus	3	6	8	3	x		x
V. vitis-idaea	3						
Aulacomnium palustre					x		
Campylopus flexuosus					x		
Dicranum scoparium	3	1				x	
Hylocomium splendens	2	4	4	2			x
Hypnum cupressiforme	5	3	1	3	x		x
Plagiothecium undulatum		1			x		
Pleurozium schreberi	8	4	1	1	x		x
Pohlia nutans				1		x	
Polytrichum commune	2	3	1				
P. piliferum			1				
Rhacomitrium lanuginosum		1					
Rhytidiadelphus loreus		1	1	1			
R. squarrosus		4	2	2	x		
Sphagnum compactum						x	
Thuidium tamariscinum				1			
Diplophyllum albicans				1			
Gymnocolea inflata						x	
Lophocolea bidentata				1			
Lophozia floerkii	1						
Cladonia coccifera				1			
C. impexa	2						
C. pyxidata	1			1			
C. sqamosa	3						
C. sylvatica		1					

The Lammermuir list is taken from Harper (1962) and Fig. 4 in this paper shows well the preference of Juncus squarrosus, with Calluna dominant throughout, for the moister podsols with deeper H horizons (17 - 28 cm.). Eriophorum vaginatum is confined to soils with H horizons deeper than 23 cm., and becomes dominant where this is greater than 28 cm. In well-grown typical heath Juncus squarrosus is absent, but where competition from ericoid shrubs is reduced, by burning, grazing, treading or any other cause, Juncus squarrosus is able to colonise the moist acid habitat, and it is to be found somewhere on most heaths. Thus it is recorded from Somerset heaths (the Quantocks, Brendons and Blackdowns), the sandy heaths in E. Dorset and W. Hampshire, the Delamere Forest in Cheshire and Skipwith Common in Yorkshire (Watson, 1932). On the North York Moors it occurs on both podsols and peat if wet, especially after heather burning (Elgee, 1912). At Blubberhouses (W. Yorkshire) Juncus squarrosus patches on Calluna moor have a similar pH and electric potential (3.5 and454) to typical Calluna around (3.4 and 527) (Pearsall, 1938).

A further habitat for Juncus squarrosus is in dune slacks e.g. on Walney Island (Pearsall, 1934) and at Winterton in Norfolk.

Juncus squarrosus in Western Blanket Bog. (Table 6.20)

Juncus squarrosus occurs in 8 of the 21 lists given for

Table 6.20.

Lists for Western Blanket Bog in which Juncus squarrosus/occurs: Trichophorum - Eriophoretum from low levels in West Scotland, Erica tetralix bog on Cader Idris, and Molinia - Myrica swamp in S.W.Sweden. (x = present, a = abundant, d = dominant; the Swedish list contains only the more prominent species).

Place	S.W. Sweden	Cader			West Scottish Highlands					
Nodum	Molinia-Myrica	E.tetr. bog	Trich-Erioph.		Trichophorum - Eriophoretum caricetosum					
	1	1	1	2	1	2	3	4	5	6
Altitude (feet)	600	13-1500	1100	1200	1200	1000	1000	1000	800	1750
Aspect and Slope (degrees)			-	10 W	-	2	-	28 NE	3	-
Agrostis canina				2		2	2	3		
Anthoxanthum odoratum						2		3		
Carex demissa										2
C.echinata				2	7	4	2	5	3	4
C.hostiana						3				
C.nigra				2	4	5	4			
C.panicea				2	4	4	+	3		4
C.pauciflora			+				4		2	
Eriophorum angustifolium		x	2	3	4	3	4	+	4	3
E.vaginatum		x	3	2					5	
Festuca ovina		x		1	2	3		3		
Juncus acutiflorus		x								
J.bulbosus				1	3	4		3		4
J.effusus		x				2				
J.squarrosus	x	a	3	5	5	3	4	3	3	2
Luzula campestris		x				1		2		
Molinia caerulea	d	x	+	2	4		3	4	5	5
Nardus stricta		x		3	3	3	3	5		3
Sieglingia decumbens						1				
Trichophorum cespitosum	x	x	5	5	2		2		7	2
Calluna vulgaris		a	3	4	2	3	2	4	5	4
Drosera rotundifolia			+		+	1	2	1	2	1
Erica tetralix	x	d	7	5	2	5	6	6	3	4
Euphrasia sp.					2	2				2
Gentiana pneumonanthe	x									
Leontodon autumnalis										3
Listera cordata				1						
Myrica gale	d		5	4						
Narthecium ossifragum			3	3	3	4	4	2	3	5
Orchis ericetorum					2					
Pedicularis sp.					3	1				
Pinguicula vulgaris				2		2				3
Polygala serpyllifolia									2	2
Potentilla erecta	x	x			5	3	1	2	3	3
Selaginella selaginoides					3	3				3
Succisa pratensis					4	2				3
Vaccinium myrtillus								2		
Viola palustris	x	x			1			1		2

	1	1	1	2	1	2	3	4	5	6
Acrocladium cuspidatum					2	1				
A.stramineum					3					2
Aulacomnium palustre				1	2		3	3		
Breutelia chrysocoma				2		4				3
Dicranum bonjeani								2		
Drepanocladus exannulatus				1						
D.revolvens						1				
Hylocomium splendens				3	2	4	1	2		3
Hypnum cupressiforme				1		4		3	2	1
Mnium punctatum				1				2		
Plagiothecium undulatum				3				1		
Pleurozium schreberi				2		4	1	2		
Polytrichum alpestre								3		
P.commune		x						2		
Pseudoscleropodium purum										3
Rhacomitrium lanuginosum		x		+		3			3	1
Rhytidiadelphus loreus				3						
R.squarrosus					1					2
Sphagnum compactum									3	
S.imbricatum	x									
S.magellanicum			3							
S.palustre								8		3
S.papillosum	x		8	6		4	4	+	7	5
S.plumulosum		a	7	5		2	5	7	6	4
S.recurvum							8	+		
S.squarrosum										1
S.subsecundum				3	3	4			3	3
S.tenellum			3						4	
Thuidium tamariscinum								2		
Aneura sp.					1					1
Calypogeia trichomanis			+	1	1		1	3		
Diplophyllum albicans						1			2	
Leptoscyphus anomala			2							
Lophozia quinquedentata								1		
L.ventricosa				1						
Odontoschisma sphagni			2						2	
Pellia epiphylla							1			
Pleurozia purpurea									3	
Scapania undulata						2				
Cladonia gracilis						2				
C.impexa						3			1	
C.mitis						1				
C.uncialis				1		2				

Trichophoreto - Eriophoretum in the Western Highlands, and these together with a list from Erica tetralix bog on Cader Idris (Price Evans, 1932) and a Molinia - Myrica swamp in the oceanic S.W. of Sweden (Malmer, 1961) have been placed together in Table 6.20.

Calluna vulgaris and Eriophorum vaginatum are not so dominant as in Pennine blanket bog (Calluneto - Eriophoretum), but there is a greater variety of other species and Sphagna are more prominent, suggesting that the water table is nearer to the surface and that the nutrient supply is perhaps rather greater. Other prominent species include Carex echinata, C. panicea, Eriophorum angustifolium, Molinia caerulea, Erica tetralix, Narthecium ossifragum, Potentilla erecta and Hypnum cupressiforme.

Whether Juncus squarrosus occurs naturally in this community or only when competition has been reduced by some interference such as treading, burning, draining or peat-cutting, I do not know. But McVean and Ratcliffe include Juncus squarrosus in many of their lists for Calluneto - Eriophoretum, in which it does not occur naturally in the Moor House area. Pearsall (1941), describing blanket bog in Connemara, records Juncus squarrosus only in a bog burnt probably within the 4 previous years, and in which most of the Sphagnum cover had been killed.

Wet heaths dominated by Molinia caerulea and Myrica gale, such as in the Somerset Levels (Watson, 1915) are allied to this community, and Juncus squarrosus is present.

Summary.

In upland Britain _Juncus squarrosus_ grows with a wide variety of plants in several different habitats. It occurs mostly on acid, base-deficient soils where different types of community are found according to the degree of wetness of the soil. Three types have been recognised at Moor House, and established as noda for the area, together with 2 other communities, richer in species.

The nodum on podsols and peaty podsols contains _Deschampsia flexuosa_, _Nardus stricta_, _Galium saxatile_, _Vaccinium myrtillus_, _Pleurozium schreberi_, _Polytrichum commune_, _Rhytidiadelphus squarrosus_, _Lophozia floerkii_ and _Ptilidium ciliare_, besides _Festuca ovina_ and _Lophocolea bidentata_, which are found in all the habitats of _Juncus squarrosus_ at Moor House. Under more waterlogged conditions there is a similar nodum on peaty gleys, with less _Galium_, _Vaccinium_, _Pleurozium_ _Lophozia_, but having additionally _Carex nigra_, _Aulacomnium palustre_ and _Calypogeia trichomanis_. The third nodum is the species-poor gley, containing _Agrostis tenuis_, _Anthoxanthum odoratum_, _Luzula campestris_, _Galium saxatile_, _Nardus stricta_, _Hylocomium splendens_, _Hypnum cupressiforme_ and _Rhytidiadelphus squarrosus_.

Communities of these three types are widespread in the Pennines, the Welsh Mountains, the Southern Uplands and the

Scottish Highlands. The two species-rich noda found at Moor House are less common, being confined to areas where calcareous rocks outcrop. That on gleys has Nardus stricta co-dominant, and is rich in sedges and herbs such as Cerastium holosteoides, Polygala serpyllifolia, Potentilla erecta and Trifolium repens, besides having nearly all the species of the species-poor gley nodum. In the other, on flushed peat, the important species are Anthoxanthum odoratum, Carex nigra, Festuca ovina, F. rubra, Cardamine pratensis, Trifolium repens, Acrocladium cuspidatum, Bryum pseudotriquetrum, Mnium punctatum and Philonotis fontana.

Juncus squarrosus also occurs in upland Britain in species-poor Festuca - Agrostis grassland on brown earth soils, in high-level chionophilous Nardus communities and in the western type of blanket bog with Trichophorum and Eriophorum. It is not a normal constituent of Pennine blanket bog, but occurs commonly where the dominance of Calluna has been reduced.

In the lowlands, Juncus squarrosus is confined to unreclaimed land, chiefly wet places in heaths.

SECTION VII: ECOLOGY AND DISCUSSION

The effects of various edaphic and biotic factors on *Juncus squarrosus* are described at the start of the section. This information, together with some from previous sections, is used in a discussion of the status of *Juncus squarrosus* in the communities described in the phytosociological section, and of their inter-relationships with other upland communities. Finally, there is a consideration of the economic value of *Juncus squarrosus* in the uplands, and a general discussion.

A) Edaphic influences

1. Moisture

While *Juncus squarrosus* has features characteristic of xeromorphs (abundant sclerenchyma, strongly thickened epidermal cell walls - see section 2), it is rarely found in well-drained habitats. These normally support *Festuca-Agrostis* grassland in the Moor House area, but some *Festuca-Agrostis* swards contain also plants of *Juncus squarrosus* and *Nardus stricta*, the *Juncus* plants being smaller than usual as on Hard Hill (site N) and in the House limestone grassland (site E) - see Table 5.1. Two turves from this latter site were put into boxes, and these placed in a glass frame in the garden at Moor House. After 14 weeks, both the *Juncus* and *Festuca* were obviously suffering from drought, having browned leaves. The boxes were now exposed to rain and the *Festuca* quickly recovered, but the *Juncus* shrivelled and died. It would seem reasonable to suppose therefore that any Juncus plants becoming established in well-drained soils are killed by periodic droughts. Where Juncus squarrosus and Nardus stricta occur in Festucetum it is probable that there is at least slightly impeded drainage.

At the other extreme, Juncus squarrosus suffers no apparent disadvantage from constant waterlogging. It is found in such situations in the field, and has grown well under such conditions in the laboratory. Doubtless this ability is conferred on the plant by the aerating system running down from the leaves, through the rhizome and into the roots. However, Juncus is not found in swamp communities which are regularly submerged, probably because its aerating system depends on gaseous exchange to the atmosphere through the leaves.

2. Texture

Juncus squarrosus is indifferent to soil texture, growing on anything from coarse sands to fine silts and peat, one reason being its forward growth through the soil by expansion inside the shoots.

3. Nutrient status

The composition of a plant gives some indication of the nutrients it is likely to require. Accordingly, the composition of Juncus squarrosus is given in Table 7.1, taken from Goodall and Gregory (1947), together with 6 other species found

Table 7.1. The composition of _Juncus squarrosus_, three other moorland species and three species of better grassland, giving the major nutrients expressed as % dry matter (after Goodall and Gregory).

Moorland species	Ash	SiO_2	N	P_2O_5	K_2O	CaO	MgO	Na_2O
Juncus squarrosus	3.7	0.33	1.35	0.41	1.82	0.11	0.26	0.20
Calluna vulgaris	3.2	0.64	1.4	0.39	0.67	0.64	0.47	0.08
Nardus stricta	2.9	3.56		0.41	1.40	0.13	0.17	0.05
Eriophorum vaginatum	2.5	0.49	1.6	0.50	1.00	0.24	0.28	0.07
Better-grassland species								
Deschampsia caespitosa	6.0	0.89		0.60	2.03	0.52	0.20	0.05
Festuca rubra	3.8			0.53	2.10	0.57	0.27	
Achillea millefolium	9.8			0.85	4.45	1.92	1.02	0.05

commonly in the Moor House area. Compared to plants of better soils, of which the 3 species given are typical, *Juncus squarrosus* is low in all nutrients but Na^{+}. Ca^{++} is especially low, even when compared with other moorland species, but PO_4^{---} content is fair, and the K^{+} high for a moorland-bog species.

As the amount of K^{+} available from mineral soils is usually greater than from blanket peat (though the exchangeable K^{+} values may not be greatly different), *Juncus squarrosus* will obtain its K^{+} requirements more readily on mineral soils and peaty gleys where its roots can reach down to mineral horizons than on blanket peats. Pearsall (1950) has gone so far as to say that *Juncus* 'seems to require some contact with mineral soil, even if this is a very poor one', and it is certainly true that *Juncus squarrosus* is not usually found on deep blanket peat. However, as the roots do not exceed 30 cm. in length (see p.2.1) there are many peaty gley stands (Table 6.3) in which the roots cannot reach the mineral soil. Examination of a profile at Rough Sike Head (site L) showed that the roots did not here reach the mineral soil. However, the K^{+} status at these sites is not known. Probably many experience slight flushing, being on slopes, and possibly in others a high K^{+} content has been retained in the plants and surface layers since the time when the roots were able to reach the mineral soil below.

However, greenhouse trials have shown that *Juncus* squarrosus can grow on a medium of very low K^+ content. Its absence from blanket bog is therefore due more to its inability to compete with Calluna and Eriophorum vaginatum than to the nutrient status of the peat.

McVean and Ratcliffe (1962) include Juncus squarrosus in the list of plants indifferent to soil status as judged by pH and Ca^{++} content, and this is not surprising as its Ca^{++} requirements (Table 7.1) are so low that almost any soil can supply them. Appendix 8 gives a few soil analyses, including some very low Ca^{++} contents. The higher Ca^{++} status of the species-rich gley and flushed-peat noda (analyses 8, 9 and 4) is clear.

The seedlings established from the germination trials of 1962 provided material for some simple fertiliser experiments done on the windowsill in the laboratory at Moor House and in the greenhouses at Durham. Seedling growth in the soil tins was better on the acid and limestone drift soils than on the blanket peat (descriptions on p. 4.2).

At Moor House the three soils received dressings of K_2SO_4, NH_4NO_3 and KH_2PO_4 at rates of 60 gm. K_2O/sq. m., 12.6 gm. N/sq. m., 37.7 gm. P_2O_5/sq. m. Measured against control pots, definite responses were obtained on the peat medium. Nitrogen alone appeared harmful, but when combined with phosphate there was better growth. Phosphate and potash alone also gave improved growth, but the best result was obtained from an NPK treatment. Phosphate alone, or in combination, resulted in the plants having a lighter green colour.

A further investigation of the effects of phosphate and potash was carried out in the greenhouses at Durham, using acid drift and blanket peat soil in 10 cm. pots. The fertilisers were mixed into the media at the start of the trial and a surface application was made later. Rates were approximately the same as at Moor House. No response was obtained, probably because the pots were free-standing, so that the nutrients were leached out by regular watering. It was interesting however, that many of the seedlings made fair growth in the pots given no fertiliser.

Response by Juncus squarrosus to soil nutrient status has also been shown during an experiment by A. J. P. Gore on the productivity of blanket bog at Bog End near Moor House. The Calluna-Eriophorum was removed from 16 plots, 24 ft. x 12 ft. (7.3 m. x 3.7 m.) in 1958, providing suitable conditions for seedling establishment. 8 subsequent treatments were given as shown in Table 7.2 and the 4 plots given treatments 7 and 8 were halved, one half being sown with Deschampsia flexuosa, the other with Phleum pratense. Compound fertiliser (treatment 8) was applied at 15 cwt./acre (1880 kg./ha.), and lime at 2 tons/acre (5000 kg./ha.), and in subsequent years at 15 cwt./ acre and 1 ton/acre respectively.

Table 7.2. The number of Juncus squarrosus seedlings established during five years in blanket bog plots (48 x 12 ft. - 14.6 x 3.7 m.) given different treatments. All vegetation down to the Sphagnum level was removed during the summer of 1958.

	Treatment			Established up to 1963*	
	Cutting	Sowing	Fertiliser	Total seedlings	Seedlings per unit area
1	1958 and yearly	0	0	6	6
2	1958, 1960, 1962	0	0	1	1
3	1958, 1961	0	0	4	4
4	1958, 1962	0	0	0	0
5	1958, 1963	0	0	0	0
6	1958	0	0	0	0
7	1958 and yearly	Phleum	$CaCO_3$	10	20
		Deschampsia flexuosa	0	0	0
8	1958 and yearly	Phleum	$CaCO_3$ + NPK	1	2
		Deschampsia flexuosa	NPK	10	20

* - any seedlings which germinated during 1963 are not included in these totals.

The *Calluna* and *Eriophorum* recovered rapidly after cutting, giving only short opportunities for *Juncus squarrosus* colonisation. As would be expected, there are most seedlings in the treatments (1, 7 and 8) having yearly cuttings, but possibly some seedlings became established in treatments 4 - 6, and were subsequently shaded out by the tall growth.

The numbers established in the plots given treatments 7 and 8 are interesting. The *Phleum* sward of treatment 8 is dense and tall, explaining the difference between the 1 plant established in it, and the 10 established in the less dense *Deschampsia flexuosa* sward. But in treatment 7, the *Phleum* sward is poor and open, and correspondingly 10 plants have become established. The *Deschampsia* sward is little better, but contains no plants of *Juncus*, and likewise, the plots of treatment 1, cut yearly but receiving no fertiliser, have considerably fewer seedlings per unit area than the limed plots of treatment 7. Thus it appears that both lime and compound fertiliser are assisting in seedling establishment.

The inability of *Juncus squarrosus* to compete with other species at higher nutrient levels was also shown by the classic experiments of Milton (1940 and 1947) in N. Wales. At the Llety *Molinia* site, *Juncus squarrosus* remained on the control plots throughout the 15 years of the experiments, both in the enclosed plots with controlled grazing and in the freely grazed plots. It was, however, rapidly excluded from the hay plots given lime or full fertiliser, with and without liming.

To sum up, Juncus squarrosus, unlike most other species, is able to grow under conditions of great nutrient deficiency, but shows some response to an improved nutrient supply. No intolerance of high nutrient levels has been shown, but the better growth Juncus squarrosus makes in such conditions is usually insufficient for it to compete successfully with the other species present. Probably K^+ is the nutrient most required by Juncus squarrosus, as a considerable amount is contained in the ash.

B) Biotic influences

1. Birds

As mentioned in section 3, the fruits of Juncus squarrosus are eaten by snow-buntings (Plectrophenax nivalis), which visit upland areas of N. Britain during the winter, and by red grouse (Lagopus scoticus) and perhaps other moorland game birds in Scotland. Judging from observations in the Moor House area and elsewhere in N. England, it can be said that these losses are slight and of no importance to the plant.

During the last century, geese were grazed extensively on the fells and commons of N. England (Welch and Rawes, 1964), and as goose corn (Winch, 1804) was an alternative name for the plant, it is possible that they ate the inflorescence or leaves, perhaps having a significant effect on the plant.

2. Agriculture

Juncus squarrosus is normally absent from all agricultural land but rough grazings. It cannot exist on arable land because of the time taken to reach maturity and the difficulties of seedling establishment, and in meadows because of the dense summer growth. On land now permanent pasture *Juncus squarrosus* if previously present, will have been eradicated on enclosure by the initial ploughing and sward establishment, and unable to recolonise the closed sward. Moor-burning to encourage a young growth of *Calluna* for sheep or grouse favours *Juncus squarrosus*, supplementing the effect of sheep-grazing, as described below.

3. Herbicides

Attention has recently turned to the improvement of hill pastures by 'surface treatment'. This involves destroying the original vegetation by the action of a herbicide, and resowing with a grass mixture. Charles (1962) has reviewed the methods.

Several papers have now appeared describing the susceptibilities of hill species to different weedkillers. Until the discovery of dalapon, herbicidal treatment of the tough monocotyledons of upland pastures met with little success. Thus *Juncus squarrosus* is resistant to MCPA and 2, 4-D at 32 oz. per acre (.18 gm./sq. m.) (Weed Control Handbook, 1958).

Dalapon (sodium 2,2-dichloropropionate) is applied in aqueous solution, and kills most monocotyledons, though dicotyledons are moderately resistant. It remains toxic in the soil for 4 to 6 weeks after application. King and Davies (1963) reported that at the rate of 5 lbs. per acre dalapon had no effect on Holcus lanatus, H. mollis, Carex flacca, Galium saxatile and Potentilla erecta; a slight effect on Agrostis canina, A. tenuis, Festuca ovina, F. rubra and Deschampsia flexuosa, reducing their cover by about 10%; but Molinia caerulea, Nardus stricta and Juncus squarrosus were highly susceptible. At 10 lbs. per acre Agrostis tenuis and Festuca ovina were more affected, depending on the season of application.

At Moor House, small trials were done at sites E and K, dalapon being applied at 5 and 15 lbs. per acre. Juncus squarrosus was killed, except for a few plants in the plots given the weaker treatment, and the other species reacted as described above. At site K on the blanket peat, Eriophorum spp. and Carex nigra were little affected, and subsequently spread at the expense of Juncus squarrosus. Polytrichum commune was scorched, but recovered well, and the other bryophytes appeared unaffected. At site E on the mineral soil, Festuca ovina, Agrostis tenuis and Anthoxanthum odoratum were reduced by the strong application and Luzula campestris and Galium saxatile became more prominent.

It would appear that applied at intermediate rates, dalapon can be used to improve upland swards without subsequent resowing, by selectively eliminating *Nardus* and *Juncus* to leave some form of *Festuca* grassland.

A new contact herbicide, paraquat, may prove to be more useful than dalapon. It has the advantage of being rapidly inactivated in the soil (Jones, 1962). However, notwithstanding the efficiency or otherwise of these herbicides, the cost of application on a large scale in the uplands will preclude their wide use in the present economic conditions.

4. Moles

Except at the higher levels, moles are abundant in the Moor House area on all mineral soils that are neither very stony or very gravelly. Their activities improve soil fertility and aeration (Silver and Moore, 1941) since soil from the lower horizons is brought to the surface in their hills, countering the effects of leaching.

This maintainance of the soil nutrient status will favour *Festuca* and the broad-leaved grasses rather than *Juncus* and *Nardus*, but more important is the opportunity the mole-hills provide for new species to enter the sward. A survey of hills cast up in the pasture at Moor House during 1962 and 1963 showed that *Agrostis tenuis*, *Festuca ovina*, *Cerastium holosteoides*, *Galium saxatile*, *Trifolium repens* and *Ranunculus repens* are the

Plate 11 - The recolonisation of a mole-hill. (Note Agrostis tenuis and Potentilla erecta).

Plate 12 - Newly cast-up mole-hills at the transition between Juncus squarrosus and Festuca limestone grassland.

most usual colonising species (Plate 11). The hills may be cast up in _Juncus squarrosus_ stands, either on mineral soils, or on peaty podsols and peaty gleys around mineral soils, as shown in Plate 12, whereupon these species colonise and form grassy swards replacing the _Juncus_.

During the 2 years, 10 hills with an average area of about 100 sq. in. were cast up in a narrow 100 yd. long zone of _Nardus_ and _Juncus_ around the limestone grassland of the pasture. The _Nardus-Juncus_ vegetation is on redistributed peat, and extends back to the eroding haggs of blanket peat at the periphery of the pasture. Thus mole activity is important over a long period in extending the small areas of good grassland which exist on rock outcrops free of blanket peat.

5. _Sheep_

Sheep graze other more succulent species, when these are available, in preference to _Juncus squarrosus_. However, in winter and early spring, when keep is scarce or the shorter swards buried by snow, the sheep turn to coarser species and at least in many areas, favour _Juncus squarrosus_ rather than heather.

But despite considerable defoliation, the winter-grazed plants do not appear to be adversely affected, probably because the evergreen leaves do not contribute very much to the food production of the plant during their second year of

Table 7.3. The change in composition of two Juncus squarrosus swards in the absence of sheep grazing, following exclosure in 1955. The values given are the number of points at which the species was contacted.

	Knock Fell		Hard Hill	
	1956	1962	1956	1962
Agrostis canina	6	2	-	-
A. tenuis	15	12	4	7
Deschampsia flexuosa	57	64	98	284
Festuca ovina	14	29	890	876
Nardus stricta	-	-	59	33
Other grasses	2	3	-	-
Carex bigelowii	1	1	107	69
Empetrum nigrum	-	-	27	3
Galium saxatile		7	117	104
Juncus squarrosus	64	9	152	14
Vaccinium myrtillus	6	-	31	8
Other flowering plants	1	-	-	1
Mosses	31	13	1136	764
Liverworts	12	6	257	237
Lichens	4	2	333	224
Total Points	73	73	1000	1000

photosynthesis. Sheep also nibble off the inflorescences, especially in grassy stands (see p.3.6), and at some places over half the inflorescences are removed in this way, causing considerable loss in seed production.

However, the disadvantages to the plant of sheep grazing are easily counterbalanced by the advantages, especially as many areas do not experience winter grazing. For in the majority of its stands, Juncus squarrosus would be smothered out by other species if these were not eaten by the sheep. This was first reported by Harris in 1939, who observed that a Nardus-Juncus sward in a 1 m. square cage at 500 m. on Cader Idris was overgrown by Deschampsia flexuosa and Vaccinium myrtillus in 2 years.

At Moor House, it has been found that Juncus squarrosus is much reduced after 7 years of exclosure (Welch and Rawes, 1964). Table 7.3 shows the change as measured by point quadrat analysis in the areas of Juncus squarrosus in the exclosure on Knock Fell (site A) and in the whole exclosure on Hard Hill (site N). In the Knock Fell stands, Deschampsia flexuosa was prominent before exclosure, and has since flourished, as shown in Plates 9 and 10. Festuca ovina has also increased, but almost all other species have decreased, suffering from the dense growth.

On Hard Hill, the Juncus squarrosus plants were more

Plate 9 - Section 7: A dark green area of Deschampsia flexuosa that has replaced Juncus squarrosus in an exclosure on Knock Fell (2450 ft.) seven years after the removal of sheep grazing.

Plate 10 - Close-up of the suppression of Juncus squarrosus by Deschampsia flexuosa.

scattered in a grassy sward, consisting chiefly of *Festuca ovina* - the third type of stand described in section 5. Here too, *Deschampsia flexuosa* has grown well in the absence of grazing, and the frequency of *Festuca* has remained high. Almost all other species, including *Nardus stricta* have decreased.

As mentioned previously in section 6, many of the stands belonging to the peaty gley nodum at the lower levels appear suitable for *Calluna vulgaris*, and, in some instances it is clear that stands of this nodum are derived from blanket bog by anthropogenic pressure, e.g. the trackway at site O. It is widely reported (e.g. Nicholson and Robertson, 1958; Ratcliffe, 1959) that heavy grazing pressure, and/or excessive burning, leads to the replacement of *Callunetum* by *Agrosto-Festucetum* on mineral soil, and *Eriophoretum* on blanket peat. A *Callunetum* on blanket peat near to the Moor House Reserve, but which is heavily grazed in winter has frequent patches of *Juncus squarrosus* in a sward of very short heather, abundant *Eriophorum vaginatum* and *Trichophorum caespitosum* (Welch and Rawes, in preparation). It is therefore suggested that many stands of *Juncus squarrosus* belonging to the podsol and peaty gley noda, especially on the west side of the Reserve and in other places where there is winter grazing, are a biotic modification of *Callunetum* on soils of intermediate moisture status. Ratcliffe (1959) indeed says in discussing the vegetation of the Carneddau, '*Juncetum squarrosi* is mainly the biotically produced counterpart of wet *Calluna* and *Vaccinium* heath'.

Removal of grazing from these stands would lead to the suppression of *Juncus squarrosus* by a dense growth of grasses, as on Hard Hill and Knock Fell, and then perhaps to colonisation by *Calluna* at the lower altitudes. But establishment of *Calluna* by seed into a dense sward is much less certain than its spread from pre-existing patches.

6. *Other animals*

Wether sheep grazed *Juncus squarrosus* much more than the ewes and lambs do today. Roberts (1959) says that in Snowdonia 50 years and more ago, drifts of dead *Nardus stricta* and *Juncus squarrosus*, uprooted by the wethers, could be seen against stone walls and gullies.

The fell pony kept at Moor House also grazes *Juncus squarrosus* severely, especially in the winter and spring, and beef cattle eat the plant. Where any of these animals are, or were, numerous, they have an important effect in lowering its competitive powers and reducing its vegetative spread. Other organisms using *Juncus squarrosus* as a food-plant are remarkably few, caterpillars and similar leaf-eating creatures being unknown. Frog-hoppers (Cercopidae) feed in the shoot bases, and are sometimes present in considerable numbers (Whittaker, 1963), but have no apparent effect on the plant.

The status of *Juncus squarrosus* communities and their interrelationships with other upland communities.

The foregoing paragraphs lead on naturally to a consideration of the status of the *Juncus squarrosus* communities and how they came to be established. It is clear that most are dependent on biotic influences, and equally clear from the information given in section 4 on the conditions for germination, that *Juncus squarrosus* could not become established in many of these stands at the present time.

Tallis in 1957 said the *Juncetum squarrosi* of the summit ridges of the Carneddau is the climax of a vegetational succession occurring of the softer rocks and on areas with a high water table. Ratcliffe (1959) concurs in his useful discussion of the relationships between vegetation and environment in the Carneddau, and it appears that these are similar in the Moor House area.

Where the dwarf shrubs *Calluna*, *Vaccinium* and *Empetrum* are excluded by grazing pressure, or by altitude in the case of the former, there is a series of communities depending on the soil moisture content and depth of peat or H horizon. *Festuca-Agrostis* grassland occurs on the driest soils, and *Nardus* enters where the drainage is more impeded. *Juncus squarrosus* prefers wetter soils, usually with an H horizon formed by the accumulation of mor humus. As the soil becomes wetter and the H layer thicker, so the amount of *Festuca* and *Nardus* decreases, leaving *Juncus squarrosus* as the dominant - the *Juncetum squarrosi sub-alpinum* in stands of the peaty gley nodum. Then as the depth of peat increases, *Eriophorum vaginatum* becomes co-dominant, and finally the sole dominant.

As the moisture tolerances of *Festuca*, *Nardus* and *Juncus* overlap, there are some intermediate soils that can support any single species or any combination, depending on the grazing pressure. With light grazing *Festuca* would normally be dominant, especially on the drier podsols. With heavy grazing, the sward is sufficiently open for *Juncus squarrosus* seedlings to become established, and the plants, though not well grown, can survive. Once established, *Juncus* is only excluded after several seasons without grazing, as on Hard Hill, and continued light grazing of a *Festuca*-*Juncus* sward would probably not lead to *Festuca* attaining sole dominance. The accumulation of mor humus below a *Juncus squarrosus* stand, resulting from the large amount of leaf litter produced, may lead to soil changes unfavourable to the broad-leaves species which grew in the previous grass sward. On the other hand, even with heavy grazing *Juncus* will not attain sole dominance on the drier swards.

In soils with rather more impeded drainage, however, *Juncus* plants, once established, spread steadily to form patches. The peaty podsol stands on Knock Fell, placed in the podsol nodum - sites P and T - fall into this group. Establishment in these stands may have occurred at a time of heavy grazing pressure, or possibly even when the ground was colonised after the last glaciation, Juncus communities having existed continuously since then. From early times there have been deer (Cervus elaphus Linn.) and ox (Bos taurus primigenuis Boj.) grazing on the fells (Welch and Rawes, 1964), which may have helped to prevent Festuca from suppressing Nardus and Juncus.

At the present time with medium grazing pressure on these stands, a considerable amount of Festuca and Deschampsia flexuosa, scattered plants of Agrostis canina and A. tenuis (Table 6.2) remain in the sward. But heavier grazing would no doubt result in the reduction of the palatable species and dominance by Juncus, very much reducing the agronomic value of the sward. The Scottish and Carneddau stands (Tables 6.11 and 6.12) parallel with the podsol and peaty gley noda at Moor House in other respects, having significantly greater amounts of both Agrostis species and Anthoxanthum odoratum, probably a result of lighter sheep grazing intensities in the past. In North Wales cattle and goats outnumbered sheep on the hills until the early eighteenth century (Roberts, 1959).

Similar considerations apply to the stands belonging to the 2 gley noda. The soil moisture conditions are suitable for the three dominants - *Festuca*, *Nardus* and *Juncus*, but in this case there is a preference gradient dependent on the soil nutrient status. Acidic peaty alluvial silts have abundant *Nardus* and *Juncus*, whereas *Festuca* has high cover on the less peaty, more mineral, gleys. Establishment conditions for *Juncus squarrosus* are reasonably good, since silt deposits after floods, and the hills cast up by moles, provide the necessary bare soil. Many of the species-rich gley stands are on fairly steep slopes, where downward soil movements similarly provide suitable conditions. The grazing of these swards will favour the spread of *Juncus* and *Nardus*, and a reduction in the cover of *Festuca*, unless it is of such an intensity that the *Juncus* and *Nardus* also are severely defoliated. Occasionally, tiny plants of *Juncus* are found in rich, heavily-grazed *Festuca* swards, and examination of the rhizome shows that the plants are old. It is clear that such plants are grazed down with the rest of the sward, and kept so small that the sheep cannot avoid them.

At the blanket peat extreme of the moisture gradient, the balance between *Juncus squarrosus* and *Eriophroum vaginatum* is maintained under sheep grazing, as the two plants are grazed about equally and at the same time of the year. But in the absence of grazing *Eriophorum* grows tall and shades out *Juncus squarrosus*. This is now happening in the Moor House pasture (site K), where sheep have not been wintered since 1951, and summer grazing has been much reduced.

On the other hand *Juncus* can invade *Calluna*-*Eriophorum* or pure *Eriophorum* communities on blanket peat, where the peat is bared. Churned-up peat in trackways and *Eriophorum* stands lacking *Sphagnum* but showing sheet erosion between the tussocks, e.g. site L, are being colonised in the Moor House area.

There remains only the flushed-peat nodum to be discussed. Stands of this type border flushes which at the present time are grazed intensively in the Moor House area. Perhaps this high grazing pressure, or perhaps the higher nutrient content of the peat is responsible for *Juncus* as opposed to *Calluna* or *Eriophorum* being dominant. Certainly without the grazing, the luxuriant growth of grasses would shade out *Juncus squarrosus*. Most of the swards are closed, but from time to time silt deposits will give opportunities for *Juncus squarrosus* to colonise. It is also possible that these *Juncus* stands are long-established, dating from the time when blanket bog growth ousted the scrub from the fell-sides. Recognition of *Juncus squarrosus* remains in the peat would be necessary to prove this hypothesis.

Finally, it must be mentioned that many *Juncus squarrosus* stands, especially of the podsol and peaty gley noda, are the result of recolonisation after peat erosion. The type of nodum depends on whether the colonisation took place on the mineral soil exposed below the peat, on the truncated peat, or on the redistributed peat. It has not proved possible to distinguish such secondary stands phytosociologically from stands thought to have Juncus squarrosus as their primary vegetation.

Whilst Juncus squarrosus is now abundant in the British uplands, it cannot in the past have been so widespread. At the forest maxima, Juncus must have been confined to the fell-tops above the tree-line, and to openings and streamsides within the forest. When bog growth replaced the trees, Juncus would have been able to spread only to the places where grazing kept down the growth of Calluna and grasses, and where Sphagnum growth was not so rapid as to swamp it. Thus away from the streams and well-drained soils it would be confined to the steeper slopes marginal to areas of blanket bog development. But the abundance of Calluna, the low grazing pressures and the lack of suitable habitats created by peat erosion must have resulted in Juncus squarrosus being much more local than it is today. Also, with a smaller total seed production, Juncus would be less able to colonise any suitable habitats that became available.

The great increase of Juncus squarrosus on the fells dates from the time when peat erosion began on a large scale, and the grazing pressure was intensified by the introduction of the mountain sheep. This was probably done by the Norse who came to Northern England in the early tenth century (Welch and Rawes, 1964). Peat erosion also has been long-continued. Bower (1959) believes it had already begun at the time of the Norse invasions. Thus conditions favouring Juncus squarrosus have probably existed in the Northern fells for the last thousand years.

It is clear that if the present uncontrolled grazing regime is continued, Juncus and Nardus will spread further into Festucetum on podsols and gleys. With control of grazing, i.e. intensified grazing in winter when only the unpalatable species are available, or no grazing on a sward for several years, or with a use of fertilisers to encourage grass growth, the amount of Juncus could be restricted, but the economics of these methods are doubtful. It must be accepted that if the fells are to be used for sheep-grazing, and the land above 1700 ft. could be used for little else economically, then a slow spread of Juncus squarrosus will occur. The seriousness of this change will be discussed later in the section.

The competitive ability of Juncus squarrosus.

Salisbury (1942) regards the reproductive capacity as 'a positive asset in the competitive equipment of the species which tends to ensure occupancy of the available ecological niches, and so to increase the species' frequency and abundance'. The most successful species in a genus usually have the largest output of viable seeds, often greater than the ecologically restricted species. In these, it might be expected that a larger output would be necessary to compensate for high seed mortality, but this is not the case, as in most species the output is considerably in excess of that needed for replacement of losses by death.

As the reproductive capacities of the other *Juncus* species are not known, comparisons with *Juncus squarrosus* are not possible. But it is certain that the large seed production is valuable to the plant in competing with other upland species. It results in viable seeds being present in considerable numbers in upland soils, ready to germinate when the necessary and rather specialised conditions occur.

Another asset to the plant is its ability to grow in a wide range of soil conditions, from nutrient-deficient to nutrient-rich, and from completely waterlogged to only moist. The combination of abundant leaf sclerenchyma and a root-aerating system in one plant helps to bring this about.

But the two assets have their corresponding liabilities, which limit the success of *Juncus squarrosus*, and define its ecology. The many seeds produced are very small, so that establishment is difficult and needs special conditions, and the complex anatomy is probably the reason for the slow growth and susceptibility to shading, as the ratio of photosynthetic tissue to total tissue is small.

Most important to the species, however, is its ability to spread vegetatively once established. Thus it is equipped to colonise rapidly new localities when they become available and can also maintain itself indefinitely in its existing stands.

The balance of assets and liabilities confer on *Juncus squarrosus* a competitive ability sufficient for it to have survived the periods of forest dominance and bog growth which were difficult for many species, and making it a very successful plant during the present times of bog erosion and intensive grazing.

The value of *Juncus squarrosus*.

Opinions have differed widely on the feeding value of *Juncus squarrosus*. Pearsall (1950) comments that it is the poorest in nitrogen of several moorland plants analysed, and also lime-poor, 'so that it is perhaps understandable that for most animals this is a last resort for winter grazing'. On the other hand, Stapledon and Hanley (1927) said that 'on *Festuca*-*Agrostis* and *Nardus* pastures alike, the heath rush is probably the most valuable grazing plant contributing to the herbage'. Thomas and Trinder (1947) give full analyses of *Juncus squarrosus*, showing the change in composition during the growing season (Table 7.4), and remark that 'as a quantitative supplement at opportune times - - , stool bent is of considerable value to the hill farmer'. Its evergreen nature

Table 7.4. The change in composition of *Juncus squarrosus* during the growing season, with the full analysis including trace elements, (after Thomas).

Cutting date	6:3	27:4	16:5	25:7	16:8	12:9
% dry matter						
Silica-free ash	2.94	4.03	4.26	3.68	3.12	2.79
SiO_2	0.52	0.21	0.26	0.33	0.15	0.16
CaO	0.097	0.098	0.112	0.112	0.108	0.096
P_2O_5	0.459	0.417	0.485	0.420	0.287	0.289
K_2O	1.48	2.18	2.49	1.83	1.72	1.38
Na_2O			0.211	0.208	0.190	0.168
MgO	0.213	0.237	0.283	0.266	0.274	0.254
Cl	0.668	0.867	0.665	0.583	0.604	0.563
S	0.147	0.242	0.220	0.200	0.160	0.134
parts per million						
Fe	140	146	129	107	116	155
Mn	106	165	270	280	168	162
Cu	5.19	8.62	8.09	6.49	12.76	7.15
Co	0.181	0.072	0.089	0.078	0.106	0.048

and rapid regrowth after a burn enhance its value. It is rich in Na and Cl, being comparable with good pasture grass in this respect, and much superior to any of the other common moorland plants. It is useful as a source of copper. However in most nutrients it is less rich than the species of the better grasslands.

It would seem that Juncus squarrosus is eaten by all breeds of hill sheep, though they vary in their liking for it. Whether this is due to specific differences between the breeds, or to acquired grazing habits, is uncertain. The Swaledales neglect Juncus squarrosus when any grass is available, but prefer it to Calluna. Daily sheep counts were made of a 2.7 acre (1.1 ha.) census plot on a Juncus squarrosus stand belonging to the peaty gley nodum (it was close to site H). From May, when the ewes and lambs returned to the fell, till September, there was a consistent monthly average of 1.0 sheep per acre (counting lambs as whole sheep), but for most of the time the sheep would be grazing on the grasses around the Juncus squarrosus tussocks. It is noteworthy that on an adjacent census plot on Calluna-Eriophorum-Sphagnum blanket bog, the average was only 0.1 sheep per acre (Rawes and Welch, in preparation).

South-country Cheviots are reported by Hunter (1962) as grazing Juncus squarrosus, especially in winter. Scottish

Blackface sheep favour Calluna, and graze it at all times of the year (Tribe, 1950). He also says they eat the whole of Juncus squarrosus plants down to the roots.

Milton (1953) gave values for the palatability of different species to Welsh mountain sheep on a hill grazing. He allotted marks on a scale of 1 to 10 for the amount of a species grazed relative to the amount on offer (discoloured leafage not being counted), and Juncus squarrosus was found to have a high palatability in winter and early spring (Table 7.5).

Table 7.5. Palatabilities on a scale 1 - 10 of selected species of a hill grazing in west-central Wales, (after Milton).

	winter	early spring	summer	autumn
Festuca ovina	8	7	5	7
Agrostis tenuis	10	6	9	10
Sieglingia decumbens	10	10	6	9
Juncus squarrosus	10	10	6	4
Nardus stricta		3	3	7
Calluna vulgaris	2	2	1	
Vaccinium myrtillus	4		1	2

In view of this information on palatability, the useful feeding value of Juncus squarrosus, and the number of sheep which graze on a Juncus squarrosus stand, it can be said that the slow spread of Juncus squarrosus in the hills, though detrimental to the quality of the better grazings, is not a very serious threat to the value of the uplands. Many areas with impeded drainage could support no better vegetation from the point of view of the grazier than Juncus squarrosus, and it is now thought (Hunter, 1954) that hill grazings are best managed when they offer a variety of different species, in proportions fitted to the grazing regime practised. With most breeds of hill sheep, only a small amount of Calluna is necessary, chiefly for grazing in the snow. Of the better grasslands, many are so well drained and on such shallow soils that Juncus squarrosus will never become prominent. Therefore the portion of the fell in which there is a balance between Festuca and Juncus is usually fairly small, and the loss in production caused by the spread of Juncus can not offset the benefits to the farmer being gained under the present grazing regime.

Certainly the hill grazings could be improved, were it so desired, by controlled grazing, surface treatment and fertiliser application, and often this would mean the replacement of Juncus by more nutritious, more productive grass species. But as the extra costs of improvement caused by Juncus having replaced fescue will be small in comparison to the total cost, the spread of Juncus in the meantime cannot be considered important.

Juncus squarrosus is also of value to man in forming a sward on peat which might otherside be undergoing erosion. When sheet erosion begins on areas of blanket peat supporting Eriophorum vaginatum, Juncus squarrosus is able to colonise

Plate 13 - The Meldon Hill slide, showing the surrounding vegetation which chiefly belongs to the Juncus squarrosus peaty gley nodum.

Plate 14 - Close-up of a block, showing the Juncus squarrosus sward. (Note the roots penetrating through to the base of the upturned peat block alongside).

the patches of bare peat between the tussocks, and prevent more serious erosion developing. Whilst it cannot colonise the steep slopes of eroding peat mounds, it is among the first plants appearing in the haggs, and can spread vegetatively to bind larger areas. Its resistance to grazing enhances its value as a coloniser, as other more succulent species are easily uprooted. The prevention of erosion is of special importance to the hydrologist, as eroded peat is washed into reservoirs and fills them up, and catchments with extensive erosion are more liable to flash-floods than those with a better vegetation cover.

It has also been suggested (Pearsall, 1950) that bog bursts - sensu lato - are now less frequent than formerly because of the development of coarse, matty vegetation (of the _Juncus squarrosus_ type), which offers more resistance to splitting than spongy bog-moss. This may be true, but a bog slide (Plate 13) has recently occurred at 2100 ft. (640 m.) on the slopes of Meldon Hill (see Fig. 1.1). Here the peat averaged 2 ft. (61 cm.) in depth, and most of the vegetation belonged to the peaty gley nodum of _Juncus squarrosus_ as shown in Plate 14 (Crisp, Rawes and Welch, 1964). Thus vegetation cover cannot itself overcome the inherent instability of blanket peat.

A general picture of the autecology of Juncus squarrosus has been gained from the wide variety of observations made during the three-year period of study. As the project was largely done in my spare time, no aspect of the autecology could be studied very intensively, but further work in certain directions would be repaid by a clearer understanding of the plant.

Much could be done, with the help of a growth chamber, on the factors affecting germination and establishment, but more important would be their investigation under varying field conditions. Competition experiments in the field at Moor House, though difficult to carry out, could confirm many of the hypotheses advanced in the discussion of ecology in this last section. There is also a need for long-term observations on the patches or plants of Juncus squarrosus in small areas which are subjected to a known grazing pressure; this is in fact incorporated in the research programme of the Nature Conservancy at Moor House. A better understanding of the previous status of the plant would result if Juncus squarrosus pollen could be distinguished from that of other rushes. The relationship of Coleophora alticolella and Juncus squarrosus is also of continuing interest, as even after nine years of observations further combinations of seed production, summer temperature and initial population size remain to be studied.

Finally, there is a great need for standard phytosociological methods to be applied in all the upland areas of the British Isles, so that the varied communities present could be distinguished and accurately described, and ultimately their approximate extent over the whole country ascertained. This would give a much better indication of how widely any conclusions, e.g. on the spread or value of *Juncus squarrosus*, made at one locality apply to the uplands of Britain as a whole.

SECTION VIII: SUMMARY AND CONCLUSIONS

The autecology of Juncus squarrosus has been investigated over a three-year period. Most of the research has been concentrated on the Moor House National Nature Reserve, an area of high-level moorland at the head of upper Teesdale in the north Pennines.

The plant exists in rosettes, which frequently form marked patches. Spread into the surrounding vegetation is by a lateral expansion of the new, developing shoots in the spring. Rhizome growth follows, with annual increments of 0.5 to 2.0 cm. The vascular and aerating systems are well-developed, allowing growth under a wide range of soil moisture conditions.

Very large numbers of tiny seeds are produced, which are dispersed from the capsules by wind. The number of inflorescences produced, and the number of florets per inflorescence are dependent mainly on the soil conditions and the vigour of the rosettes, climate being a secondary influence. But climate determines the number of florets that ripen to form capsules. In average years a considerable proportion of the capsules ripen up to 2,000 ft. (610 m.), but in the cool sun-deficient summer of 1962 only 25% of the florets formed capsules at 1650 ft. (503 m.). At the lower levels attack by the larvae of the Tineoid moth Coleophora alticolella Zell. significantly reduces seed production in some years.

In most seasons seed viability is high, though it falls at the highest levels. Germination required light, and normally occurs on the soil or peat surface, but experiments showed that at 73°F (23°C) slow germination occurred in the dark. By varying day length and light intensity, it was found that the effects of light were cumulative.

Seedling establishment is uncommon, except in special conditions such as at the base of eroding peat mounds, and the plants normally perpetuate themselves vegetatively. However, large numbers of dormant viable seeds are present in most upland soils, so that colonisation can take place when suitable conditions occur. Seedling growth is slow; probably five years elapse between germination and maturity.

In the Moor House area Juncus squarrosus appears to be indifferent to soil nutrient status, but it shows some response to increased nutrient supply. The Juncus squarrosus communities were examined phytosociologically and five noda were distinguished, dependent on the soil type. Festuca ovina and Lophocolea bidentata are constant associates. The noda are:-

1) the peaty gley nodum, called Juncetum squarrosi subalpinum by other workers. It is the most widespread, and Deschampsia flexuosa, Aulacomnium palustre, Polytrichum commune and Calypogeia trichomanis are prominent.

2) the podsol nodum, characterised by Pleurozium schreberi and the absence of wet-place species. Nardus stricta is

frequent, and Galium saxatile and Rhytidiadelphus squarrosus abundant in this and the next nodum.

3) the species-poor gley nodum, characterised by Agrostis tenuis and the absence of mor-humus species.

4) the species-rich gley nodum, in which Nardus and the broad-leaved grasses have high cover values.

5) the flushed-peat nodum which is of small extent and contains base-demanding and hydrophyllic species - Acrocladium cuspidatum and Mnium punctatum are the most important.

Evidence is strong that sheep grazing is responsible for the present state of these communities. Callunetum is thought to be the climax vegetation of the sites with impeded drainage, though the immediate effect of the removal of grazing from the present stands is the spread of Eriophorum vaginatum, or Festuca ovina and Deschampsia flexuosa, depending on the moisture status.

Where drainage is free, Juncus squarrosus is never well-grown, and could not become dominant even under heavy grazing. On grassy swards of intermediate moisture status, grazing is favouring the spread of Juncus squarrosus and Nardus stricta at the expense of the more nutritious Festuca ovina and Agrostis tenuis. But Juncus squarrosus has some nutritional value to the grazing animal, and because grass species are also present, stands of *Juncus* seem preferable agronomically to Callunetum in the area studied. Therefore the slow spread of *Juncus* in certain of the better swards cannot be considered a very serious threat to the value of the uplands.

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Appendix 1. *Juncus squarrosus* reproductive capacity in 1962 and 1963 at the Moor House sites

Site	Altitude (feet)	No. of Quadrats	Infl./Q. (1/4 sq.m.)	%Eaten	Caps./Infl.	%Caps. of florets	Seeds/Q.	Seeds/Caps.	Year
G fell-top podsol near summit of Cross Fell, amongst polygons	2925	18	16.1	57.9	0	0	0	0	1962
			5.0	22.2	0.0014	0.02	1.3	12	1963
A peaty podsol over calcareous drift on Knock Fell	2450	20	24.7	1.2	0	0	0	0	1962
			16.7	3.3	0.12	1.6	14	7	1963
L blanket peat dominated by *Erioph. vaginatum* at Rough Sike Head	2300	15	32.6	0.04	0.03	0.43	5	5	1962
		14	9.8	0	1.1	19.0	100	9	1963
J recolonisation complex on House Hill	1900	20	21.5	2.6	0.54	5.2	132	12	1962
			19.6	1.0	5.1	48.8			1963
I initial stage of recolonisation by *Juncus squarrosus* on House Hill	1900	10	48.1	2.9	0.14	1.8	105	17	1962
		9	27.4 -	1.2	5.5	54.2			1963
C alluvial gley by Moss Burn and Nether Hearth Sike	1850	20	14.4	9.4	1.34	9.5	177	11	1962
			17.2	9.9	6.6	60.3			1963
E brown earths and podsols on drift over limestone around Moor House	1850	20	6.5	14.7	0.25	2.5	26	19	1962
			8.0	1.3	4.8	49.5			1963
K blanket peat in Moor House pasture dominated by *Eriophorum vaginatum*	1850	20	22.0	0.23	0.51	4.3	93	8	1962
			18.4	0.27	6.0	62.1			1963
H peaty podsol on green slopes below blanket bog on Sike Hill and Bog Hill	1800	20	14.4	0	0.54	5.7	70	10	1962
			21.3	1.9	6.1	51.0			1963
D Leat bank - drift exposed about 200 years ago = gley. by Trout Beck	1775	20	8.7	32.4	1.45	12.4	99	12	1962
			12.2	17.6	7.9	58.7			1963
B alluvial gley at the junction of the Tees and Trout Beck	1750	20	32.4	16.2	0.25	3.9	70	10	1962
			41.4	43.4	4.0	48.9			1963
F podsols and peaty podsols over whinsill at Dipper Bridge over Tyne	1550	20	11.6	0.4	7.09	52.3	415	5	1962
			14.7	0	8.7	61.4			1963

- 1 quadrat missed here which had very many inflorescences in the previous year.

Appendix 2. Reproductive capacity in 1961 on Tees - Cross Fell transect

As no effort was made to collect every inflorescence in a given area, the value for fls./infl. is probably a little high. With random collection small inflorescences may have been missed. Collected 10:9:61.

A = alluvial soil, E = edge of blanket peat, usually a peaty podsol.

Site	Altitude (feet)	No. of Infl.	Average Height (cm.)	Florets/ Infl.	% Caps. of Florets	Total Seeds obtained	Seeds/ Capsule
junction of Trout Beck and Tees (= B)	1750 A	48	26	9.0	52	1500	6.6
	1750 E	48	30	7.8	35	720	5.4
up the Tees	1975 A	41	28	10.8	19.5	320	3.7
	1975 E	34	28	11.8	29	560	4.8
at the foot of the final steep rise of the Tees	2250 A	19	28	17.4	21	250	3.5
	2250 E	40	30	14.7	26	580	4.1
Tees Head	2500	61	25	12.3	4	50	1.6
(27:10:61)		42	27	14.7	2.4	100	6.7
S.E. slope of Cross Fell - podsol	2650	24	20	8.0	0	0	0
- peaty podsol	2725	53	25	10.9	0.04	15	7.5
Top plateau, some distance from summit	2900	52	15	6.3	0	0	0
Top plateau, close to summit (27:10:61)	2925	32	17	3.7	0.85	5	5

Appendix 3. Reproductive capacity results for Pendle Hill in 1961 and 1963, with 95% confidence limits. Collected in September in both years. The 1961 inflorescence number is the total collected.

Site and Description	Altitude (feet)	Infl./Q. 1/4 sq.m.	Av.Height (cm.)	%Eaten	Fls./ Infl.	Caps./ Infl.	%Caps.of Florets	Seeds/ Caps.	Year
S.E. escarpment of Pendle: a steep slope with a very bouldery soil, probably recolonised scree. A bracken zone below - the lower two stations are by a wide track where treading has kept down the bracken. Above is a zone of abundant _Vaccinium myrtillus_ and _Festuca_	1150	(21)	12	33.0	4.0±1.2	1.9	46.0	1.5	1961
		23.5		17.0	7.6±0.9	1.8	23.7		1963
	1350	(38)	16	57.9	2.5±0.3	1.1	42.5	0.6	1961
		12.0		72.2	7.1±1.8	1.5	21.1		1963
	1550	(39)	17	56.4	2.6±0.7	0.7	27.3	1.7	1961
		26.0		34.6	4.7±0.8	0.6	11.9		1963
Edge of top plateau: a peaty podsol where blanket peat passes into scree grassland.	1750	(52)	16	40.4	4.8±0.9	2.0	42.6	1.6	1961
		34.0		42.7	6.3±0.9	2.7	42.4		1963
Top plateau: on eroded blanket peat	1750	(52)	18	21.3	9.0±1.6	1.0	10.9		1961
		60.5		51.3	7.3±0.9	4.3	58.4		1963
Top plateau: recolonised area after peat removal at summit	1830	(57)	16	52.6	3.7±0.8	0.3	9.0	2.8	1961
		55.5		69.4	5.0±0.9	3.0	60.9		1963

Appendix 4. Reproductive capacity results for various sites, 1961-1963, with 95% confidence limits. % infested values are bracketed when it is likely that they are less than the maximum.

Date	Site and Description	Altitude (feet)	No. of Infl.	%Eaten	Fls./Infl.	Caps./Infl.	%Caps. of Florets	%Infested of Capsules
28: 9:61	Enclosed pasture opposite Lee House, Tynehead	1400	36		22.7	9.1	40	33.4
1:10:62	Hill House rough pasture (base of <u>Coleophora</u> transect of Durham zoologists)	1450	123	0	15.6±1.02	6.20±0.87	39.8	(1.6)
1:10:62	Dipper (= site F, harvested 11:8:62)	1550	137	0	13.8±1.21	6.97±0.87	50.7	(4.1)
26:10:62	Dipper		113			6.00±0.70		9.1
27: 9:63	Dipper		65		13.4±0.97	10.4	77.3	0.9
27: 9:63	Dorthgill	1500	53		11.6±0.92	6.8	59.0	1.7
28: 9:61	peaty podsol by roadside above the Snead	1650	43		10.1	3.5	35	14.4
27: 9:63	" "		49		12.5±1.00	7.4	58.9	0.28
			36		19.5±1.9	8.6	44.1	0.65
20: 8:62	iron podsol on Jeffrey Fell, Longridge (Lancs.) <u>Calluna</u> with <u>Molinia</u> and <u>Vaccinium myrtillus</u>	700	61	0		1.9		(3.5)
17: 9:63			108	45.3	11.4	3.3	29.1	9.0
5: 9:62	Peaty gley on Tatham Fell (Yorks) near source of Hodder abd. <u>Js</u> with much <u>Polytrichum commune</u> and some <u>Nardus</u>, <u>Juncus effusus</u> and <u>Eriophorum vaginatum</u>	1000	20	0	7.8±2.21	3.35±1.08	43.2	(0)
22:10:62	Podsol on West side of Buckstones Moss (Yorks). <u>Nardus</u> dominant, some <u>Molinia</u> tussocks and <u>Vaccinium</u> and <u>Empetrum</u>.	1050	56	0	8.5±1.47	5.21±1.44	61.1	3.8
6:11:62	peaty podsol with <u>Nardus</u> and <u>Molinia</u> at Moel Eilio (Caerns.)	1200	37	18.9	10.3±1.46	6.70±1.48	64.9	7.5
8:11:62	enclosed field by Preston-Bolton road over Belmont at Withnell. Chiefly <u>Nardus</u>, with some <u>Juncus effusus</u> and <u>Deschampsia flexuosa</u>. <u>Molinia</u> tussocks grazed down by cows	850	62	69.4	6.1±1.81	3.58±1.40	59.1	5.9
3: 9:63	podsol near Braemore Lodge (Wester Ross)	900	54	0	12.8±1.31	7.1	55.6	5.7
21: 9:63	peaty podsol at Harris End (Lancs.)	530	77	1.3	11.9±0.75	6.5	54.7	7.4

Soil profiles and their nomenclature (after Ragg).

Name	Horizon	Description
Iron Podsol	L and F	Partial and undecomposed plant litter.
	H	less than 10cm. dark brown or black humus (mor type).
	A	soil dark above, paler below, not gleyed.
	B1	absent or thin and soft.
	B2	orange-brown enriched layer, not gleyed.
	B3	relatively enriched.
	C	relatively unweathered parent material.
Peaty Podsol	L and F	
	H	dark brown or black raw humus from 5 to 100cm. thick.
	A	soil dark above with humus incorporated, paler below with signs of gleying.
	B1	thin iron pan, sometimes hard.
	B2 and 3	brighter layers with sesquioxide enrichment; no signs of gleying.
	C	relatively unweathered parent material.
Peaty Gley (= peaty gleyed podsol or gleyed podsol)	L and F	
	H	dark brown or black raw humus from 5 to 100cm. thick.
	A	dark above, paler below; gleyed throughout, sometimes with ochreous mottling.
	B1	absent or soft.
	B2 and 3	dark-coloured and gleyed.
	C	parent material but still gleyed.
Gley (= non-calcareous gley)	L and F	
	H	a trace or absent.
	A	dark gleyed mineral layers, with moder humus above, paler below; has no free calcium carbonate.
	B	dark gleyed mineral layers.
	C	parent material with original colour more apparent, still gleyed.
Brown Earth (= brown forest soil)		
	L and F	
	H	a trace or absent.
	A	crumby, brown with moder humus incorporated.
	B2	brighter brown with some sesquioxide enrichment.
	B3	less brown, nearing parent material in colour.
	C	relatively unweathered parent material.
Blanket Peat.	L and F	
	H	over 100cm. (1 ft.).
	A and B	waterlogged.

Notes about the plant tables.

Cover values shown in the tables are according to the Domin scale thus:-

10	cover about 100%
9	cover more than 75%
8	cover 50-75%
7	cover 33-50%
6	cover 25-33%
5	abundant, cover about 20%
4	abundant, cover about 5%
3	scattered, cover small
2	v. scattered, cover small
1	scarce, cover small
x	isolated or depauperate.

McVean and Ratcliffe do not use the last category x in the Scottish Highland list, but use + for species occurring just outside the quadrat. These have not been noted at Moor House.

Quadrat size:

the Moor House quadrats are all 50 x 50 cm. except for 3 large ones, of $4m.^2$ in each nodum.

the Scottish Highland quadrats are all $4m.^2$ except for the following:-

Table 6.11, list 1 is $10m.^2$
5, 6 are $2m^2$

6.13, list 1 is $8m.^2$
2 is $2m.^2$

the Carneddau quadrats are all of 25 x 25 cm., but different numbers have been taken to get the average cover value thus:-

Table	6.11	- 40 quadrats
	6.12	- 20 quadrats, except lists 1 and 4 which are 10.
	6.13	- 20 quadrats
	6.19	- 20, 20 and 25 quadrats respectively.

Species delimitation:

Luzula campestris includes L. multiflora and L. campestris.

Epilobium anagallidifolium includes what has been called E. palustre elsewhere, since the Moor House plants resemble E. palustre but authorities have named them E. anagallidifolium.

to keep down table size *Sphagnum* species have been aggregated according to the plan in Dixon (1924) Student's Handbook of British Mosses. Thus *S. plumulosum* includes *S. acutifolium*, *S. capillaceum*, *S. girgensohnii*, *S. nemoreum*, *S. quinquefarium*, *S. rubellum*, *S. russowii*.

S. squarrosum includes *S. teres*

S. subsecundum includes *S. auriculatum* and *S. contortum*

Species nomenclature is from:-

flowering plants - Clapham, A. R., Tutin, T. G., and Warburg, E. F. (1962) Flora of the British Isles. Cambridge.

mosses - Watson, E. V. (1955) British Mosses and Liverworts. Cambridge.

liverworts - MacVicar, S. M. (1926) The Student's Handbook of British Hepatics. 2nd edition. Eastbourne.

lichens - Watson, W. (1953) Census Catalogue of British Lichens. Cambridge.

The species in the tables of section 6 have been divided into the following groups:-

grasses, sedges and rushes
other vascular plants, including ferns, horsetails and clubmosses

mosses
liverworts
lichens

Appendix 7.

Locations of the Scottish Highland lists

Table	Community		Location
6.11	spp-poor Js	1-3,5-7	Ben Lawers, Perthshire
		4	Sgurr a' Chaorachain, Monar Forest, Ross.
		8	Allt Slanaidh, Glen Tilt, Perthshire
		9	A'Bhuid-heanach, Laggan, Inverness-shire
		10	Creag Meagaidh, Laggan
6.12	Js bog	1	Meall Horn, Reay Forest, Sutherland
		2	Sgurr na Feartaig, Achnashellach, Ross.
6.13	spp-poor Ns	1-3	Ben Lawers, Perthshire
6.14	" "	1	Ben Lawers, Perthshire
		2	Allt Slanaidh, Glen Tilt, Perthshire
	spp-rich Ns	1	Ben Lui, Argyll
		2	Carn Gorm, Glen Lyon, Perthshire
		3	Inverinain Burn, Glen Lyon
		4	Cairn Derg, Glen Clova, Angus
		5	Corrie Burn, Clova, Angus
		6	Braedonie, Clova, Angus
		7	Glen Fiadh, Clova, Angus
6.15	spp-rich Js	1	Inverinain Burn, Glen Lyon, Perthshire
		2	Ben Lui, Argyll
		3	Carn Gorm, Glen Lyon, Perthshire
6.16	Carex-Sax.	1	Sgurr a' Ghlas Leathaid, Strath Bran, Ross.
	Hypno-Caric. alpinum	1	Meall na Samhna, Glen Lochay, Perthshire
		2	Glas Maol. Perthshire
		3	Sgurr na Laparch, Glen Cannich, Inverness-shire
		4	Carn an Tuirc, Glen Clunie, Aberdeenshire
		5	Ben Lui, Argyll
		6	Sgurr nan Ceannaichean, Achnashellach, Ross.
	J.acuti-Acro.	1	Milton of Clova, Argyll
		2	Inverar, Glen Lyon, Perthshire
	spp-rich Ns	1	Creag Meagaidh, Perthshire
	spp-poor Ns	1	Mullach na Maorle, Glen Cannich, Inverness-shire
		2	Beinn Tarsuinn, Letterewe, Ross.
	Sphagno-Caric sub-alpinum	1	Moulzie Burn, Clova, Angus
		2	Glen Markie, Monadhliath, Inverness-shire
		3	Carn Gorm, Glen Lyon, Perthshire
		4	Meall Ghaordie, Breadalbane, Perthshire
		5	Beinn Enaiglair, Inverlael, Ross.
		6	Abernethy Forest, Inverness-shire
	alpinum	1	Meikle Kilrannoch, Clova, Angus
	Js bog	1	A'Bhuidheanach, Laggan, Inverness-shire

Table	Community		Location
6.17	Agr-Fest.	1	Ben Klibreck, Sutherland
		2	Eididh nan Clach Geala, Inverlael Forest, Ross.
		3	Beinn Enaiglair, Braemore, Ross.
		4	Beinn Odhar Mhor, Glen Finnan, Inverness-shire
		5	Allt a' Chonais, Achnashellach, Ross.
		6-7	Creag Meagaidh, Laggan, Inverness-shire
		8	Fionehra, Isle of Rhum
		9	Allt a'Mhudaidh, Fannich Forest, Ross.
	Alch-Agr-Fest.	1	Beinn Odhar Mhor, Glen Finnan, Inverness-shire
		2	Coire Chuirn, Drumochter, Inverness-shire
6.18	Nard-Trich.	1-3	Beinn Eighe, Ross.
	Trich-Ns.	1	Creag Meagaidh, Laggan, Inverness-shire
	Ns-Pleur.	1	Beinn Evnaich, Dalmally, Argyll
		2	Beinn Fhada, Kintail, Ross.
	Vacc.-Ns.	1	Carn Ban, Freevater Forest, Ross.
6.19	Callunetum	1	Druim Cholozie, Glen Murck, Aberdeenshire
6.20	Trich-E.vag.	1	Glen Markie, Monadhliath, Inverness-shire
		2	Markie Burn, Monadhliath
	Trich-E.vag.	1	Mullach na Maoile, Glen Cannich, Inverness-shire
	caricetosum	2	Glen Markie, Monadhliath, Inverness-shire
		3	Glen Banchor, Inverness-shire
		4	White Haugh, Clova, Angus
		5	Sgurr Dubh, Coulin, Ross
		6	Beinn Enaiglair, Braemor, Ross.