U6
Juncus squarrosus-Festuca ovina grassland

Synonymy
Retrogressive *Eriophoretum* Adamson 1918 *p.p.*; *Festuca-Juncus squarrosus* grassland Ratcliffe 1959*a*; *Juncetum squarrosi sub-alpinum* McVean & Ratcliffe 1962; *Juncus squarrosus* bog McVean & Ratcliffe 1962 *p.p.*; *Juncus-Vaccinium myrtillus* nodum Welch 1967; *Juncus-Carex nigra-Polytrichum commune* nodum Welch 1967; Species-poor *Juncus-Nardus* nodum Welch 1967; Species-poor *Juncetum squarrosi sub-alpinum* Eddy *et al.* 1969; Species-poor *Nardetum sub-alpinum*, *Juncus* facies Eddy *et al.* 1969; *Juncus squarrosus* nodum Edgell 1969; *Festuca ovina-Juncus squarrosus* sociation Edgell 1969; *Nardo-Juncetum squarrosi* Birks 1973, Evans *et al.* 1977, Hill & Evans 1978, *p.p.*; *Junco squarrosi-Festucetum tenuifoliae* Birse & Robertson 1976, Birse 1980, 1984.

Constant species
Festuca ovina, *Juncus squarrosus*, *Polytrichum commune*, *Lophocolea bidentata s.l.*

Rare species
Barbilophozia lycopodioides.

Physiognomy
The *Juncus squarrosus-Festuca ovina* grassland includes most of the sub-alpine vegetation in which *Juncus squarrosus* occurs abundantly among a diversity of bog, grassland or heath associates. Early stages in colonisation can have a rather patchy cover of the rush and, in less favourable situations, it can remain more sparse, but typically it is at least co-dominant, and its tight, squarrose rosettes are often very numerous. Sometimes, the cover consists of colonies of various sizes, expanding marginally at a slow rate, clumps at Moor House of 4 m diameter being aged at over 160 years; in other cases, the sward is more uniform and sometimes quite dense. Each spring, new shoots burst out rapidly from among the old, bringing a flush of fresh glossy green to the herbage, after which the plants flower and the old foliage dies (Welch 1966*b*).

The most usual co-dominants are grasses, particularly *Festuca ovina*, with *F. vivipara* occasionally distinguished at higher altitudes and, rather less commonly and not usually so abundant, *Deschampsia flexuosa*. Both of these can occur scattered among the *J. squarrosus* plants or as patches in mosaics with its clumps and, whereas the rush is generally ignored by grazing stock, these grasses are often cropped short, providing a valuable bite, particularly where the community occurs around the margins of bogs at higher altitudes. Other grasses are not quite so frequent, although *Agrostis canina*, particularly ssp. *canina*, is characteristic of wetter peats and, over poorly-drained peaty podzols, there is often some *Nardus stricta*, *Agrostis capillaris* and *Anthoxanthum odoratum*. The commonest sedge is *Carex nigra*, which generally follows *A. canina* ssp. *canina* in its distribution through the community, and with these species, too, there can be some *Eriophorum angustifolium* or *E. vaginatum*, the latter sometimes with local abundance, particularly over the run-down or recolonising fringes of blanket peat, where it may attain co-dominance with the rush in what has sometimes been called *Juncus squarrosus* bog (McVean & Ratcliffe 1962, Welch 1967). *Carex bigelowii* is occasionally found in heathier stands and large clones can be prominent in transitions to certain kinds of *Nardus-Carex* snow-bed.

The only other important vascular plant through the community is *Vaccinium myrtillus* which can be very common on the less waterlogged soils, though even then it is usually found at fairly low covers. Other sub-shrubs are scarce, *Calluna vulgaris* occurring very occasionally, *Empetrium nigrum* and *Vaccinium vitis-idaea* rarely. The only common herbaceous dicotyledons are *Galium saxatile* and *Potentilla erecta*, although there can be local modest enrichment with plants characteristic of bogs or flushed calcifuge swards.

Bryophytes are not always of high cover, but they are quite often numerous. *Polytrichum commune* is the commonest moss throughout and the one which most often makes an abundant contribution, forming patches among the vascular plants that can be quite extensive on

wetter peats, and sometimes being accompanied there by a variety of Sphagna. In other cases, it is *Dicranum scoparium* and pleurocarpous mosses such as *Hypnum cupressiforme*, *Rhytidiadelphus squarrosus*, *Pleurozium schreberi* and *Hylocomium splendens* that are the more abundant members of this element. Then, there are frequently some leafy hepatics with small strands of *Lophocolea bidentata s.l.* and, rather less commonly, *Ptilidium ciliare* growing among the rushes and grasses, and *Calypogeia trichomanis* (probably including at least some *C. fissa*) and *Barbilophozia floerkii* occurring on bare peat.

Lichens are uncommon but some heathy stands have a locally varied cover among which *Cladonia arbuscula*, *C. furcata* and *Cetraria islandica* are the commonest species.

Sub-communities

***Sphagnum* spp. sub-community:** *Juncus squarrosus* bog McVean & Ratcliffe 1962 *p.p.*; *Juncus-Carex nigra-Polytrichum commune* nodum Welch 1967 *p.p.*; Species poor *Junceteum squarrosi sub-alpinum* Eddy *et al.* 1969 *p.p.*; *Nardo-Juncetum squarrosi* Birks 1973 *p.p. J. squarrosus* is typically very abundant in this sub-community with *F. ovina* generally of only moderate cover, quite often sparse and sometimes absent altogether. *D. flexuosa* is also much patchier than usual, with *Nardus*, *Agrostis capillaris* and *Anthoxanthum* only occasional and of low cover. *Agrostis canina*, however, and *Carex nigra* are both frequent, though not usually abundant, and there is sometimes a little *Eriophorum angustifolium* or *E. vaginatum*, scattered through the sward or locally prominent in patchy mosaics, the former thickening up in damp hollows or shallow pools, the latter becoming more abundant in transitions to intact blanket bog. Upstanding peat blocks or drier banks may have some *V. myrtillus*, *Calluna* or *Empetrum nigrum* and there can be occasional *Galium saxatile* and *Potentilla erecta*.

Bryophyte cover is usually extensive, with *P. commune* at its peak of frequency and abundance here, and common records also for *L. bidentata s.l.*, *P. ciliare* and, preferential to this sub-community, *Lophozia ventricosa*. *C. trichomanis* is occasional and there is also sometimes a little *Aulacomnium palustre*. Most striking of all, though, is the occurrence of various Sphagna, often in locally prominent patches, with *S. recurvum* most frequent, *S. capillifolium*, *S. papillosum*, *S. cuspidatum*, *S. palustre* and *S. russowii* more occasional. *Mylia anomala* can sometimes be found among the clumps and wet hollows can also have some *Drepanocladus fluitans* or *Calliergon stramineum*.

***Carex nigra-Calypogeia trichomanis* sub-community:** *Juncus-Carex nigra-Polytrichum commune* nodum Welch 1967 *p.p.*; Species-poor *Juncetum squarrosi sub-alpinum* Eddy *et al.* 1969 *p.p.*; *Juncus squarrosus* nodum Edgell 1969 *p.p. J. squarrosus* is usually abundant here, though quite often co-dominant with *F. ovina* or, less commonly with *D. flexuosa* or mixtures of the two grasses. *Agrostis canina*, *Carex nigra* and *Eriophorum angustifolium* all remain common, though only the sedge attains moderate cover and then not very often. *E. vaginatum* is occasional and again locally abundant in stands which grade to the *Sphagnum* sub-community. In other cases, *Galium saxatile*, *Potentilla erecta*, sparse *V. myrtillus* and occasional *Nardus* occur in vegetation transitional to heathier stands.

Among the bryophytes, *P. commune* remains very common and it is sometimes abundant, and there is frequently some *L. bidentata s.l.*, *C. trichomanis*, *P. ciliare* and, preferentially here, *Plagiothecium undulatum*. *Aulacomnium palustre* is often found, particularly on the wetter peats, where small patches of Sphagna also sometimes occur. In somewhat drier situations, *Rhytidiadelphus squarrosus* and *Pleurozium schreberi* become more frequent, with occasional *R. loreus*.

***Vaccinium myrtillus* sub-community:** Retrogressive *Eriophoretum* Adamson 1918 *p.p.*; *Juncus-Vaccinium myrtillus* nodum Welch 1967; *Juncus squarrosus* nodum Edgell 1969 *p.p.*; *Festuca ovina-Juncus squarrosus* sociation Edgell 1969; *Junco squarrosi-Festucetum tenuifoliae* Birse & Robertson 1976 *p.p. J. squarrosus* and *F. ovina* are usually co-dominant in this sub-community, with *D. flexuosa* also very common and sometimes of moderately high cover. *Nardus* and *Agrostis capillaris* occur occasionally in small amounts but *A. canina* and *Carex nigra* are much reduced in frequency. Most distinctive is the frequent occurrence of *V. myrtillus*, usually as sparse sprigs but occasionally showing local abundance, and along with this *Carex bigelowii* is quite common, sometimes growing in prominent clonal clumps. Then, *Galium saxatile* is much more frequent than in the previous sub-communities and on occasion it forms noticeable patches.

Polytrichum commune remains very common, though it is generally sparse and more characteristic is the high frequency of *Dicranum scoparium*, *Hypnum cupressiforme* and *Rhytidiadelphus squarrosus* with occasional *R. loreus*, and of the leafy hepatics *Ptilidium ciliare*, *Barbilophozia* spp. and, in some localities in northern Britain, the rare *B. lycopodioides*. Some stands also have a variety of lichens, individually not usually of high cover, but together giving the vegetation a distinctive stamp: *Cetraria islandica*, *Cladonia arbuscula* and *C. furcata* are the commonest of these, with occasional *C. impexa*, *C. pyxidata* and *Cornicularia aculeata*.

***Agrostis capillaris-Luzula multiflora* sub-community:** Retrogressive *Eriophoretum* Adamson 1918 *p.p.*; *Fes-*

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tuca-Juncus squarrosus grassland Ratcliffe 1959*a*; *Juncetum squarrosi sub-alpinum* McVean & Ratcliffe 1962; Species-poor *Juncus-Nardus* nodum Welch 1967; Species-poor *Nardetum sub-alpinum*, *Juncus* facies Eddy *et al.* 1969; *Junco squarrosi-Festucetum tenuifoliae* Birse & Robertson 1976 *p.p.*; *Junco squarrosi-Festucetum tenuifoliae*, Typical subassociation Birse 1980 *p.p.*; *Nardo-Juncetum squarrosi* Evans *et al.* 1977, Hill & Evans 1978, *p.p.* Again, *J. squarrosus* and *F. ovina* are generally co-dominant with *Agrostis capillaris* and *Nardus* preferentially frequent and sometimes of moderately high cover. *Anthoxanthum* and *Luzula multiflora* also attain their peak of frequency here, though they are usually only sparse in the sward. *Agrostis canina* and *Carex nigra* occur only very occasionally, but *V. myrtillus* is also absent and there is generally no *C. bigelowii*. *Galium saxatile* remains common but some stands also have scattered herbs of more mesophytic or flushed swards such as *Trifolium repens*, *Achillea millefolium*, *A. ptarmica*, *Cardamine pratensis* and *Equisetum palustre* or even, where the irrigating waters are a little more calcareous, *Thymus praecox*.

Among the bryophytes, *P. commune* is unusually infrequent but *Rhytidiadelphus squarrosus* and *Hypnum cupressiforme* are often joined by *Hylocomium splendens* with occasional *Pleurozium schreberi* and *Plagiothecium undulatum* and, along with *Lophocolea bidentata s.l.*, there is sometimes a little *Barbilophozia floerkii*.

Habitat

The *Juncus-Festuca* grassland is characteristic of moist peats and peaty mineral soils, almost always base-poor and infertile, over gentle slopes and plateaus at higher altitudes in the cool and wet north and west of Britain. Climate and soils have a marked effect on the composition of the community, but this is very often a secondary vegetation type, strongly encouraged by particular kinds of grazing and burning treatments through damper upland pastures and on the drying fringes of blanket mires.

J. squarrosus is a shade-sensitive, generally hydrophilous and mildly calcifuge plant that contributes to many kinds of short herbaceous and sub-shrub vegetation on moist peaty soils through the less continental parts of north-west Europe. In this country, it occurs in the warmer and drier lowlands of the south and east where locally impeded drainage or flushing maintains otherwise suitable soils in a drought-free state throughout the year, so it is essentially a plant of wet heaths and the margins of valley bogs. By contrast, to the north and west, where the mean annual maximum temperature is less than 27 °C (Conolly & Dahl 1970) and where the annual rainfall exceeds 1000 mm (*Climatological Atlas* 1952) with more than 160 wet days yr^{-1} (Ratcliffe 1968), the cool humid climate maintains congenial soil conditions over a very wide area and the rush is much more universally distributed (Perring & Walters 1962), being found from sea-level to over 1000 m (Welch 1966*b*) in a great variety of short damp grasslands, heaths and mires.

In the more equable parts of its range in the north and west, at lower altitudes generally and particularly towards the more oceanic western seaboard, *J. squarrosus* often makes its most obvious contribution in vegetation with much *Molinia caerulea* and *Scirpus cespitosus*, frequently heathy, sometimes grassy, sometimes transitional to blanket bog. In this scheme, such mixtures fall mostly within the *Scirpus-Erica* wet heath. The *Juncus-Festuca* grassland, by contrast, though it encompasses as great a variety of vegetation, is a community of higher altitudes, being generally found between 400 and 800 m, where the temperatures are becoming somewhat inhospitable for *Molinia*. In the very rainy and cloudy conditions characteristic of such altitudes, suitably wet peaty soils can be maintained over a wide variety of substrates, even pervious and somewhat calcareous ones, on slopes of up to 15° or so. Towards such limits, the *Juncus-Festuca* grassland extends some way on to peaty podzols, which can be quite free-draining but where the humose topsoil is kept permanently moist by the high atmospheric humidity and often also by some flushing with waters draining from the hills above. The deposition of heavy-textured drift over such ground or the accumulation of clayey solifluction debris on gentler slopes often adds a measure of drainage impedence to the profiles or encourages flushing, and the community occurs widely on stagnohumic gleys and humic stagnopodzols developed from such materials. Very commonly, soils of these kinds form intergrades on shelving ground to the ombrogenous peats that mantle the summit plateaus, watersheds and dip slopes of our higher hills, and the *Juncus-Festuca* grassland forms some of its most extensive stands over shallower peats of this kind, where there is seasonal or sometimes virtually continuous waterlogging, or on deeper deposits that have dried out somewhat. Almost always, the soils in these various situations are base-poor, with a superficial pH generally between 3.5 and 5, which means that there is a usually unrelieved calcifuge character to the vegetation. Locally, irrigation can bring some base-enrichment, as where flushing waters drain off calcareous rocks or drift on higher ground, a feature well seen through the Breadalbane Mountains, where some grassier stands of the community occur on peaty silts with a pH above 5 and measurable amounts of calcium in the profile (McVean & Ratcliffe 1962, Welch 1966*b*, 1967). Even here, however, the calcicolous element in the flora is subdued and the vegetation can readily be accommodated in the *Agrostis-Luzula* sub-community; most of the more obviously basiphile swards where *J. squarrosus*

occurs with such plants as *Carex panicea*, *C. pulicaris* and *Selaginella selaginoides* are best placed in the *Nardus-Galium* grassland.

Although the vegetative vigour and fertility of *J. squarrosus* are impaired towards the higher altitudinal limits of the *Juncus-Festuca* grassland where the summers are short and cool (Pearsall 1950, Welch 1966*a*), the rush can maintain fairly good growth across much of this spread of soil types away from the extremes of droughting and submergence (Welch 1966*b*) and, unlike *Nardus*, it does not suffer by having its roots out of contact with a mineral substratum on deeper peats, a point of great ecological significance in the contribution which the two plants make to our poorer-quality grazings. But the considerable variety of edaphic conditions, particularly the differences in drainage, has a marked effect on the associated floras and many of the contrasts between the sub-communities can be related to this and other soil factors. At one extreme, on the more free-draining profiles such as podzols with but modest gleying, flushed soils or peaty alluvium on the terraces of small hill streams, the *Vaccinium* and *Agrostis-Luzula* sub-communities are characteristic, with the kind of flora usually associated with Myrtillion heaths or Nardo-Galion grasslands. Indeed, in the *Agrostis-Luzula* swards, beneath which the organic content of the soils tends to be at a minimum for the community, the vegetation grades continuously into the *Nardus-Galium* grassland, typically a community of mineral soils with a moist humic top, with fine-leaved upland pasture grasses such as *Agrostis capillaris*, *Anthoxanthum* and *Nardus* itself, together with the pleurocarpous mosses characteristic of this rough herbage, making their maximum contribution to the *Juncus-Festuca* grassland. The soils here are peaty enough for the typical small *Luzula* of the swards to be *L. multiflora* rather than *L. campestris*, but *P. commune* and the mire plants well represented on more waterlogged soils perform badly. The *Vaccinium* sub-community shows considerable edaphic overlap with the *Agrostis-Luzula* type and, among patchworks of different kinds of *Juncus-Festuca* grassland, it can likewise pick out the better-quality mineral-based soils, a feature well seen at Moor House (Welch 1966*b*, 1967, Eddy *et al.* 1969) and on Cader Idris (Edgell 1969). Indeed, in many situations, the contrasts in floristics and structure between these two sub-communities are attributable as much to variations in the treatments they have received as to differences in soils (see below). But very commonly, the *Vaccinium* type extends further on to shallower peats proper, or even on to quite deep deposits that have become dried out superficially, something that is very clear around the margins of run-down blanket bogs through the southern Pennines (Adamson 1918, Tansley 1939). Apart from *F. ovina*, then, *D. flexuosa* is often the most common grass among the *V. myrtillus* and the cryptogam flora is of the kind associated with short heathy vegetation on mor or with patches of bare peat. Towards higher altitudes, the appearance of *C. bigelowii* in this kind of *Juncus-Festuca* grassland provides a clear link with montane heaths.

With the shift on to more strongly gleyed or flushed peaty soils and seasonally wet peats, the *Carex-Calypogeia* sub-community is the characteristic type, an extensive kind of vegetation over uneroded intergrades to blanket bogs, which can run on to deeper deposits along trackways or where there is recolonisation of moist surfaces after burning (e.g. Welch 1967, Eddy *et al.* 1969, Edgell 1969). *D. flexuosa* often retains some vigour on the less thoroughly waterlogged of these soils, but the extinction of *V. myrtillus*, the patchiness of *F. ovina* and the increased frequency of *Carex nigra* and *Agrostis canina* ssp. *canina* are very characteristic of the generally wetter edaphic conditions. Here, too, there appears that sporadic representation of *Eriophorum vaginatum* and *E. angustifolium* that is very characteristic of the fringes of blanket bog, either running down to *Juncus-Festuca* grassland or redeveloping through it to patchy Erico-Sphagnion mire. The *Sphagnum* sub-community represents the limit of variation in this direction, where the floristics of the *Carex-Calypogeia* type are supplemented by the local occurrence of clumps of Sphagna and a few other mire plants. This kind of *Juncus-Festuca* vegetation, more a bog than a grassland, has been recorded in the very wet north-west of Scotland (McVean & Ratcliffe 1962) but it also occurs where blanket bog remnants persist among recolonising *J. squarrosus*, or where re-establishment is advanced enough for the mosses to appear once more: even then, it is often *Sphagnum recurvum*, rather than the typical species of the intact bog plane, that is most characteristic.

In all these situations, *J. squarrosus* is often dependent upon treatments of various kinds to establish, spread and maintain itself in the abundance characteristic of the vegetation included here. In favourable circumstances, the rush can set formidable quantities of seed, around 10,000 m^{-2} from a normal stand at one estimate (Welch 1966*a*), but the number of inflorescences produced, the quantity of seed set, their ripening and viability all decline with increasing altitude and in unfavourable seasons (Pearsall 1950, Welch 1966*a*). Moreover, at lower levels, the increased seed production is often balanced to some extent by losses to the larvae of the moth *Coleophora alticolella* (Jordan 1958, 1962, Reay 1964, Welch 1965). Dispersal is by wind (Welch 1966*b*) and perhaps also in the wet wool of sheep (Pearsall 1950), but old inflorescences often decay with some seed still in the capsules. Germination is light-dependent and, for successful establishment, the seedlings need bare but stable areas of suitable soils, not

subject to frost-heave or rain-wash, taking more than a year to gain a firm hold (Welch 1966*b*). Provided there is a ready seed source to hand, then, which there often is in the adjacent grasslands, *J. squarrosus* is well able to capitalise upon the appearance of any patches of bare peat or humic soils. These may slump down where there is solifluction or be washed out of flushes, or be exposed more extensively around the margins of blanket bogs that have gradually dried or been drained, and where the demise of the mire vegetation has been hastened by burning. Adamson's (1918) account of the retrogression of *Eriophorum vaginatum* mire in the southern Pennines shows well the place of the *Vaccinium* sub-community of the *Juncus-Festuca* vegetation in this process of run-down, and the description and map of Moor House (Welch 1967, Eddy *et al.* 1969) provide a typical illustration of the complex patchworks of the *Vaccinium*, *Carex-Calypogeia* and *Sphagnum* sub-communities that can develop over bared peats of varying degrees of wetness on and around blanket bogs that have been long subject to burning and grazing.

Once established in such situations, *J. squarrosus* can persist long and increase its cover by slow vegetative spread: indeed, at higher altitudes, this must be the main means of expansion from the colonies that originate from infrequent episodes of seeding in. The rush can survive to some degree in the wet-heath and blanket-mire vegetation that may redevelop with the colonisation of such sites (Eddy *et al.* 1969), but it will not stand being heavily shaded. Very often, then, grazing plays a crucial role in maintaining the *Juncus-Festuca* community in such situations by keeping the swards short and setting back the vigorous growth of sub-shrubs like *V. myrtillus* and particularly *Calluna*. *J. squarrosus* itself is not very palatable, being rather tough and fibrous, but the leaves are eaten by cattle and ponies, and by sheep when herbage is scarce in winter and early spring (Milton 1953, Welch 1966*b*); indeed, all-winter wethers will set into the plant at leaf initiation, biting out the centres (Roberts 1959). But, by and large, it is not affected adversely by grazing or the attendant treading, and it can benefit greatly where other elements in the swards are selectively cropped. And even the less luxuriant vegetation included in the community can be quite attractive to the stock, generally now breeding ewes, which have open access to the hill slopes over which it can be found, the presence of the frequent tufts of *F. ovina* and *D. flexuosa* among the rush providing a good bite. At Moor House, for example, stocking rates of 1–2 sheep of all ages ha^{-1} were reported during the summer months on stands of the *Carex-Calypogeia* sub-community, very much higher than on the neighbouring *Calluna-Eriophorum* mire (Welch 1966*b*, Eddy *et al.* 1969). And the effect of withdrawing such grazing was strikingly shown in enclosure experiments at this site, where, after just seven years, *J. squarrosus* was almost totally suppressed by the upgrowth of these two associated grasses in a stand of the *Vaccinium* sub-community (Welch & Rawes 1964, Rawes 1983).

It is on the somewhat drier soils favoured by this kind of *Juncus-Festuca* vegetation, and by the *Agrostis-Luzula* type, that the impact of grazing variations on the community is most obvious. In fact, over peaty mineral soils, much of the floristic and structural contrast between these two sub-communities may be due to differences in pastoral treatments, the more mixed grassy swards of the *Agrostis-Luzula* type being favoured by heavier and closer cropping. Interactions between grazing intensity and soil conditions are probably also of prime importance in controlling the boundary between this kind of *Juncus-Festuca* vegetation and the closely similar *Nardus-Galium* and *Festuca-Agrostis-Galium* grasslands. The spread of *J. squarrosus* in upland pastures, like that of *Nardus*, tends to be encouraged where uncontrolled, heavy and selective grazing has been applied over more ill-draining ground, so it is likely that some of the grassier stands of the *Juncus-Festuca* community subsist in situations where, with a different grazing regime, there could be better-quality *Festuca-Agrostis-Galium* grassland. *J. squarrosus* is not so narrowly confined edaphically as *Nardus*, which favours moist humic soils with a mineral base in which it can root, so it can dominate in many tracts of hill grazings where *Nardus* is at a strong disadvantage, but on the kinds of gleyed or flushed peaty soils characteristic of the *Agrostis-Luzula* sub-community, the balance between the two species is perhaps fine. In such situations, heavier grazing probably favours *Nardus*, because *J. squarrosus* is rather more palatable and is fairly readily overwhelmed by the build-up of litter and mor that characteristically occurs amongst *Nardus* tussocks.

Zonation and succession

The community occurs widely with other kinds of grassland and with heaths and mires in vegetation patterns where edaphic differences and treatments are the major controlling variables. Although it is not true to say that *J. squarrosus* is never a constituent of climax vegetation (cf. Welch 1966*b*), the kind of abundance that it shows here is under the strong influence of biotic factors and, in most situations, the *Juncus-Festuca* grassland is clearly an anthropogenic replacement for other types of vegetation.

The clearest soil-related zonations involving the community are seen where the wet peaty profiles that it favours occur in sequences running from free-draining acidic mineral soils through to ombrogenous peats. Often, in such patterns, the *Juncus-Festuca* grassland grades, over moist peaty podzols, disposed over steeper slopes or more pervious ground, to some sort of *Nardus-Galium* grassland, the boundary between the vegetation types being frequently a matter of the dominance of

either *J. squarrosus* or *Nardus* against a background flora that can remain more or less uniform throughout. Thus, the *Agrostis-Luzula* and *Vaccinium* sub-communities of the *Juncus-Festuca* grassland can pass almost imperceptibly into Species-poor *Nardus-Galium* grassland, with a variety of fine-leaved grasses, *V. myrtillus* and pleurocarpous mosses frequent right through the swards. Or, on more strongly gleyed or flushed soils, or over shallow redistributed peats of varying degrees of wetness, there can be a continous zonation from the *Carex-Calypogeia* type of *Juncus-Festuca* grassland to the *Agrostis-Polytrichum* sub-community of the *Nardus-Galium* grassland, with *Agrostis canina*, *Carex nigra*, *Polytrichum commune* and *Ptilidium ciliare* common overall. Frequently, too, the *Nardus-Galium* grassland passes in turn to the *Festuca-Agrostis-Galium* grassland, typically a vegetation type of free-draining podzolic soils and base-poor brown earths, but extending in its *Vaccinium-Nardus* sub-community on to moister and more humic profiles. *J. squarrosus* does run on into such vegetation as an occasional associate and sometimes there can be a direct transition from the *Juncus-Festuca* community to the *Festuca-Agrostis-Galium* grassland marked by a fairly sharp reduction in the abundance of the rush.

In the opposite direction in this kind of zonation, the *Juncus-Festuca* grassland often gives way, with varying degrees of abruptness, to some type of blanket-mire vegetation developed over ombrogenous peats that thicken up with the move on to gently-sloping or flat ground. Typically, through the range of the community, this is the *Calluna-Eriophorum* bog or, in the southern Pennines and locally elsewhere, the very impoverished *Eriophorum* bog. With the gradual increase in peat depth and wetness over graded transitions to level ground, the *Carex-Calypogeia* and *Sphagnum* sub-communities can form a fairly gentle, uninterrupted zonation to such mire types, with species such as *Eriophorum vaginatum*, *E. angustifolium*, *Scirpus cespitosus* and the Sphagna becoming more important in the vegetation on moving towards the intact mire plane. And, in some cases, there is an intervening belt of Ericion wet heath, usually of the *Scirpus-Erica* type, the *Vaccinium* sub-community of which can make the transition between the grassland and the mire even more gradual and protracted.

Complete patterns of this kind, uncomplicated by topographic variation or too many confusions deriving from treatments, are rare, but they can be seen in broad outline over many slopes and summits through the range of the community. Sometimes, the vegetation types are disposed over ground of increasing height and lessening slope so as to form a broad altitudinal zonation, a pattern clearly visible over the rounded tops of the Moorfoot and Moffat Hills (Smith 1918) in the Southern Uplands, on the terraced scenery of the Pennines (Adamson 1918, Eddy *et al.* 1969) and over some of the less calcareous mountains through the Breadalbane range, as on Meall Ghaordie and Meall Na Samhna (Ratcliffe 1977). In more rugged scenery, like that of the Carneddau (Ratcliffe 1959*a*) and Cader Idris (Edgell 1969) in Wales, the patterns tend to be more complex and fragmented and, over the craggy high ground of the north-west Highlands, the community becomes distinctly infrequent, though the massively-rounded watersheds of Beann Dearg and Seana Bhraig show a characteristic zonation (Ratcliffe 1977). In this more oceanic part of the uplands, too, there is a strong tendency for suitably gentle ground, which is usually to be found over the stepped landscape at lower altitudes, to have vegetation with much *Molinia* over the wet peats around the fringes of blanket mire. Here, zonations with the *Molinia-Potentilla* mire, *Molinia*-dominated *Scirpus-Erica* wet heath and the *Scirpus-Eriophorum* mire present an oceanic equivalent to patterns with the *Juncus-Festuca* community from less equable parts of the north and west and, in some localities, mixed sequences with elements of both kinds of transition can be found.

A variety of other complexities is often seen. For one thing, natural drying of the peats around the margins of many of our high-level blanket mires, frequently exacerbated by draining, burning and pollution, has resulted in many places in baffling patchworks of eroding and recolonising bog, wet heath, and *Juncus-Festuca* and *Nardus-Galium* grasslands over fragments of intact mire and redistributed peat washed down over the slopes below. This kind of pattern is shown to perfection on the map of Moor House produced by Eddy *et al.* (1969). Then, the zonations described above are frequently cut through by vegetation types which pick out seepage lines, flushes, water-tracks and streams. The *Juncus-Festuca* grassland can itself mark such sites within tracts of drier grasslands, occurring over irrigated ground and along the periodically-flooded terraces of streams, but often it occurs as a transitional zone around stands of soligenous mire vegetation on the more or less permanently waterlogged peats and humic gleys. The commonest pattern of this kind involves the *Carex echinata-Sphagnum* mire, the most widespread of our sub-montane sedge- or rush-dominated base-poor flushes and the *Carex-Nardus* sub-community of that vegetation can grade continuously with the *Carex-Calypogeia* sub-community of the *Juncus-Festuca* grassland, such species as *A. canina*, *C. nigra*, *J. squarrosus*, *F. ovina* and *P. commune* occurring throughout, but with a noticeable increase in poor-fen herbs and Sphagna in moving on to wetter ground. Again, this kind of zonation is well shown on the map of Moor House (Eddy *et al.* 1969) and on that from Cader Idris (Edgell 1969).

Further complexities occur where such irrigation brings a measure of base-enrichment, something that is widely seen on the hills between Breadalbane and Clova,

where there is seepage from Dalradian Limestone and calcareous metasediments, through those parts of the Pennines where Carboniferous Limestone or drift derived from it are important elements in the landscape and, more locally, where there is seepage from limy partings among shales and sandstones or calcareous intrusions. In such situations, well-defined flushes are generally occupied by the strikingly calcicolous *Pinguiculo-Caricetum* or, on higher ground, by the *Carici-Saxifragetum*, but, where the water trickles through *Juncus-Festuca* vegetation, there can be a flushed zone of the *Agrostis-Luzula* sub-community with a moderately basiphile character. In other cases, the *Carex* sub-community of the *Nardus-Galium* grassland, sometimes with locally abundant *J. squarrosus*, can also occur on the irrigated ground and, where there are more free-draining lime-rich soils on the slopes around, the *Festuca-Agrostis-Galium* grassland is replaced there by the *Festuca-Agrostis-Thymus* grassland. The flanks of Ben Lawers have good patterns of this kind with the more calcifuge zonations to soligenous mires occurring in close proximity (Ratcliffe 1977).

Then there are the effects of treatments, which interact with the edaphic influences over the full range of soils on which the *Juncus-Festuca* vegetation occurs. On exposed slopes at higher altitudes, the community sometimes grades, through the *Vaccinium* sub-community, to wind-blasted heath maintained by harsh climatic conditions, but for the most part it is an anthropogenic vegetation type whose general abundance over wet, peaty ground through the hill pastures of the north and west is a reflection of the spread of *J. squarrosus* in damp swards with uncontrolled, selective grazing. Even on soils which are just moist, such treatment may still give the plant a strong competitive edge against many of the fine-leaved grasses of calcifuge swards though, being a little more palatable than *Nardus*, it probably loses out to this plant where both species are at home edaphically. However, where heavy grazing has been combined with burning over wet heaths and blanket mires, a commonplace through many upland areas, the *Juncus-Festuca* community can extend into situations which would never support vigorous *Nardus-Galium* grassland. By affecting balances of this kind, complex histories of land use, involving episodes of burning and local variations in grazing intensity, have undoubtedly played a large part in the development of the patchworks of vegetation seen in places like Moor House (Welch 1967, Eddy *et al.* 1969).

Reversing the advance of *J. squarrosus* by manipulations of continued grazing is difficult, particularly in the severely run-down landscape of eroded bog margins. Among grasslands, Milton (1940) showed how, with a shift to the kind of heavy grazing, trampling and dunging that cattle and ponies provide, the abundance of both *J. squarrosus* and *Nardus* can be reduced in the type of vegetation included here, but achieving this over extensive tracts of hill land without damaging the better-quality swards in the mosaic is another matter. Relaxation of grazing, on the other hand, is a readier way of eliminating *J. squarrosus* because, unlike *Nardus*, its squarrose rosettes are readily overwhelmed by taller herbage and the accumulation of litter. In the enclosure experiments at Moor House, for example, the rush was all but eliminated from the *Vaccinium* sub-community by tussocky growth of *D. flexuosa* and *F. ovina* after just seven years of protection, while, in vegetation approximating to the *Carex-Calypogeia* type, *Eriophorum vaginatum* and *D. flexuosa* completely extinguished it after a decade (Welch & Rawes 1964, Rawes 1981). On peats such as those of this latter site, the *Calluna-Eriophorum* mire is probably the natural climax vegetation, though reversion to impoverished *Eriophorum* mire is perhaps more likely over drying blanket-bog fringes (Ratcliffe 1959*a*, Rawes 1981). Over thinner deposits and redistributed peat, the likely successor with reduction of grazing is some sort of *Scirpus-Erica* wet heath, perhaps the *Vaccinium* type with its mixtures of *V. myrtillus*, *Erica tetralix* and *Calluna* with *J. squarrosus*, *Nardus* and occasional small fine-leaved grasses and pleurocarps. Then, over peaty mineral soils, the *Juncus-Festuca* grassland may revert to *Vaccinium-Deschampsia* heath, the *Alchemilla-Carex* sub-community of which comes close in its floristics to the *Agrostis-Luzula* and *Vaccinium* sub-communities here. Throughout its range, the *Juncus-Festuca* vegetation is found with these different kinds of heath in mosaics which are probably controlled mainly by differences in grazing intensity and frequency of burning. Towards lower altitudes and over soils which are not too wet or impoverished, it is possible that withdrawal of grazing from such patchworks could permit succession through heath to forest, perhaps some kind of *Betula-Molinia* or *Quercus-Betula-Dicranum* woodland, but this is unlikely over more inhospitable ground at higher altitudes.

Distribution

The *Juncus-Festuca* community occurs widely through the uplands of Britain, though it becomes scarcer in the north-west Highlands where it is generally represented by the *Carex-Calypogeia* and *Sphagnum* sub-communities. Otherwise the different kinds of vegetation included here seem to occur throughout the range, their abundance determined by interactions between soils and treatments.

Affinities

Early accounts of vegetation with much *J. squarrosus* (Adamson 1918, Pearsall 1950, Ratcliffe 1959*a*) helped

provide a basis for understanding the ecology of the rush in sub-alpine anthropogenic pastures, but it was not until the work of McVean & Ratcliffe (1962) that details were available of the floristic composition of some of these swards over an extensive area of the uplands. The distinction which these authors drew between a *Juncetum squarrosi* and *J. squarrosus* bog was filled out very clearly in the studies of Welch (1966*b*) and Eddy *et al.* (1969) at Moor House, and their noda appear to provide an adequate framework for much of the variation to be seen elsewhere among the vegetation with this plant.

As with McVean & Ratcliffe (1962), a separation is made here between distinct communities dominated by *J. squarrosus* or *Nardus*. Although the two plants show considerable overlap in their edaphic preferences and a similar response to particular treatments, being associated in certain kinds of poor-quality pasture with much the same flora, a single *Nardo-Juncetum*, as favoured by Birks (1973), Evans *et al.* (1977) and Hill & Evans (1978), or a compendious *Junco-Festucetum*, as proposed by Birse & Robertson (1976, also Birse 1980, 1984), would be far too cumbersome to incorporate all the swards in which these species, alone or together, have an important role.

Elsewhere in Europe, communities with *J. squarrosus* have been described from southern Scandinavia (Nordhagen 1922), the Faroes (Hansen 1967), Germany (Tüxen 1955, Oberdorfer 1978), Belgium (LeBrun *et al.* 1949), The Netherlands (Westhoff & den Held 1969), France (Stieperaere 1978) and Spain (Rodriguez 1966). Sometimes, these are of a grassier composition, in other cases more like wet heath, variation which reflects the diversity of our own swards with the rush, but often the vegetation is more species-rich than it is here, with *Pedicularis sylvatica* and *Polygala serpyllifolia*, occasionally *Gentiana pneumonanthe*, being characteristic (Ellenberg 1978, Stieperaere 1978). In certain schemes, such vegetation types have been incorporated in the Ericion tetralicis alliance of wet heaths (where these character species are in fact found with us), but mostly they are located in a Juncion squarrosi within the Nardetalia. Despite the impoverished nature of British *J. squarrosus* vegetation, this seems the most sensible place for the *Juncus-Festuca* community.

Floristic table U6

	a	b
Juncus squarrosus	V (4–10)	V (4–10)
Festuca ovina	V (1–6)	V (1–6)
Lophocolea bidentata s.l.	IV (1–4)	IV (1–4)
Polytrichum commune	V (1–6)	V (1–6)
Carex nigra	IV (1–4)	IV (1–4)
Agrostis canina	III (1–4)	III (1–4)
Eriophorum vaginatum	II (1–4)	II (1–4)
Eriophorum angustifolium	II (1–3)	II (1–4)
Sphagnum palustre	I (1–3)	I (1–6)
Sphagnum cuspidatum	I (1–3)	I (1–3)
Scirpus cespitosus	I (4–6)	I (1–6)
Calliergon stramineum	I (1–3)	I (1–3)
Sphagnum recurvum	IV (1–8)	I (1–4)
Lophozia ventricosa	III (1–4)	I (1–3)
Sphagnum capillifolium	II (2–4)	I (1)
Sphagnum papillosum	II (2–8)	
Drepanocladus fluitans	II (1–3)	
Mylia anomala	I (1–3)	
Narthecium ossifragum	I (1–3)	
Calypogeia trichomanis	II (1–3)	IV (1–3)
Plagiothecium undulatum	II (1–3)	III (1–4)
Aulacomnium palustre	II (1–4)	III (1–4)
Deschampsia flexuosa	II (1–3)	IV (1–6)
Ptilidium ciliare	III (1–3)	III (1–4)
Pleurozium schreberi	II (1–4)	III (1–3)
Vaccinium myrtillus	I (1–4)	I (1–3)
Barbilophozia floerkii	I (1–3)	II (1–4)
Dicranum scoparium	I (1)	I (1–3)
Carex bigelowii		
Rhytidiadelphus loreus	I (1–3)	II (1–3)

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c	d	6
V (1–10)	V (4–10)	V (1–10)
V (1–8)	V (4–6)	V (1–8)
IV (1–3)	IV (1–4)	IV (1–4)
IV (1–8)	II (1–4)	IV (1–8)
II (1–4)	II (1–3)	III (1–4)
II (1–4)	I (1–3)	II (1–4)
I (1–4)		I (1–4)
		I (1–4)
		I (1–6)
		I (1–3)
		I (1–6)
		I (1–3)
		I (1–8)
I (1–4)	I (1–3)	I (1–4)
		I (1–4)
		I (2–8)
		I (1–3)
		I (1–3)
		I (1–3)
I (1)	II (1–3)	II (1–3)
II (1–4)	II (1–3)	II (1–4)
I (1–3)		I (1–4)
IV (1–6)	I (1)	III (1–6)
IV (1–4)		II (1–4)
IV (1–6)	II (1–3)	III (1–6)
V (1–6)		II (1–6)
IV (1–6)	II (1–3)	II (1–6)
III (1–4)	I (1–3)	II (1–4)
III (1–4)		II (1–4)
II (1–6)		I (1–6)

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Cladonia impexa	I (1)		II (1–4)		I (1–4)
Cladonia arbuscula		I (1)	II (1–4)		I (1–4)
Cladonia furcata		I (1)	II (1–3)		I (1–3)
Barbilophozia lycopodiodes			II (1–3)	I (1–3)	I (1–3)
Cetraria islandica			II (1–3)		I (1–3)
Cornicularia aculeata			II (1–3)		I (1–3)
Rhytidiadelphus squarrosus	I (4)	III (1–4)	IV (1–4)	V (1–3)	III (1–4)
Galium saxatile	II (1–3)	II (1–4)	IV (1–6)	V (1–4)	III (1–6)
Hypnum cupressiforme	I (1)	II (1–3)	III (1–3)	V (1–4)	II (1–4)
Agrostis capillaris	I (1)	I (1)	II (1–4)	V (1–4)	II (1–4)
Nardus stricta	II (1–6)	II (1–6)	II (1–6)	IV (1–6)	II (1–6)
Luzula multiflora	I (1)	I (1–3)	I (1–3)	V (1–3)	I (1–3)
Hylocomium splendens	I (1–3)	I (1–3)	I (1–3)	V (1–3)	I (1–3)
Anthoxanthum odoratum	II (1–3)	I (1–3)	I (1–4)	IV (1–3)	I (1–4)
Achillea ptarmica				II (1–3)	I (1–3)
Cardamine pratensis				II (1–3)	I (1–3)
Trifolium repens				II (1–3)	I (1–3)
Achillea millefolium				II (1–3)	I (1–3)
Equisetum palustre				II (1–3)	I (1–3)
Potentilla erecta	II (1–4)	II (1–3)	II (1–4)	II (1–4)	II (1–4)
Pohlia nutans	I (1–3)	I (1–3)	I (1)	I (1)	I (1–3)
Calluna vulgaris	I (1–4)	I (1–3)	I (1–6)		I (1–6)
Number of samples	18	76	86	19	199
Number of species/sample	15 (7–36)	14 (7–29)	15 (7–28)	16 (10–22)	15 (7–36)
Vegetation height (cm)	13 (6–20)	22 (20–25)	14 (4–30)	25	15 (4–30)
Vegetation cover (%)	75	no data	no data	no data	
Altitude (m)	589 (351–810)	545 (285–760)	706 (380–892)	534 (457–570)	612 (285–892)
Slope (°)	5 (0–20)	2 (0–12)	4 (0–45)	4 (1–7)	3 (0–45)

a *Sphagnum* sub-community
b *Carex nigra-Calypogeia trichomanis* sub-community
c *Vaccinium myrtillus* sub-community
d *Agrostis capillaris-Luzula multiflora* sub-community
6 *Juncus squarrosus-Festuca ovina* grassland (total)

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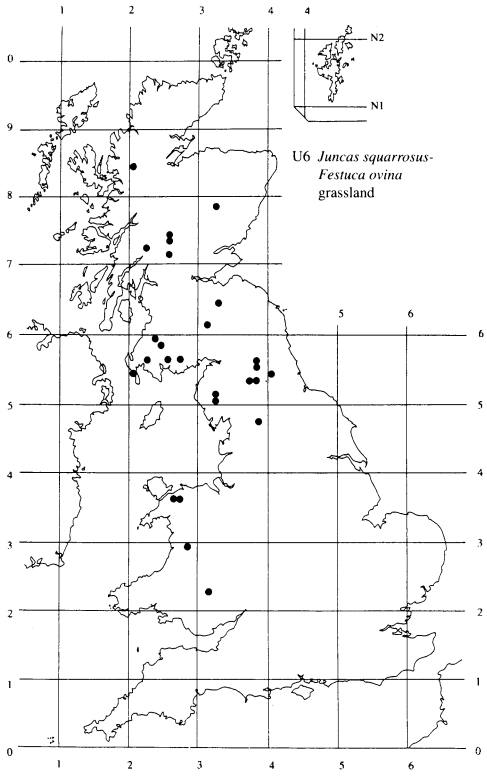

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