U5
Nardus stricta-Galium saxatile grassland

Synonymy

Nardetum strictae Smith & Moss 1903, Smith & Rankin 1903, Lewis 1904*a*,*b*, Moss 1911, Tansley 1939; Grass moor Smith 1911 *p.p*; *Nardus-Deschampsia* grassland Adamson 1918; Marginal *Nardetum* Smith 1918; *Nardetum* Price Evans 1932; *Festuca-Nardus-Juncus squarrosus* Grassland Ratcliffe 1959*a*; *Nardetum sub-alpinum* McVean & Ratcliffe 1962, Meek 1976, Ferreira 1978; *Nardus-Trichophorum* nodum McVean & Ratcliffe 1962 *p.p.*; Type A *Nardus stricta/Festuca ovina/Deschampsia flexuosa* grassland King 1962; *Nardus-Festuca-Deschampsia* Type 2 grassland King & Nicholson 1964; Species-rich *Juncus-Nardus* nodum Welch 1967; Species-poor *Nardetum sub-alpinum* Eddy *et al.* 1969; *Nardus stricta* 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 *p.p.*; *Nardus stricta-Anthoxanthum odoratum* nodum Huntley 1979; *Cirsium palustre-Nardus stricta* Community Birse 1980.

Constant species

Agrostis capillaris, *Festuca ovina/vivipara*, *Galium saxatile*, *Nardus stricta*, *Potentilla erecta*, *Rhytidiadelphus squarrosus*.

Physiognomy

The *Nardus stricta-Galium saxatile* grassland includes most of the grassier vegetation in which *Nardus stricta* plays a prominent role. *Nardus* is usually the most abundant plant in these swards, often dominant, sometimes overwhelmingly so, its structural importance helping to separate the community from similar grasslands in which it is a frequent companion, but at lower cover. In typical stands, the distinctive habit of this grass gives the vegetation a quite unmistakable stamp and exerts a controlling influence on the variety and distribution of the associates. The physiognomy is a densely tufted one, with the shoots tightly packed and congested below with the persistent remains of the tough, basal sheaths, new growth being crowded in among the old to build up tussocks of sometimes substantial size. These develop on shortly-branching, superficial rhizomes which grow fairly slowly and eventually die from behind, expanding the colony marginally as a thick sod of closely-spaced tussocks accumulating humose detritus between them. Vigorous growth of this kind can oust most other potential dominants, although the developing peaty topsoil can provide a congenial substrate for a range of smaller herbs and bryophytes. Characteristically, the *Nardus* itself maintains contact with the underlying mineral substrate by means of thick roots (Smith 1918, Chadwick 1960, Pearsall 1968).

Even where *Nardus* is more patchy here, its pale wiry foliage, left untouched by most stock, helps mark out stands of the community even from a distance, particularly as winter approaches, when the leaves turn from grey-green to a bleached straw colour. But close observation of the sward almost always reveals the presence of some other smaller grasses, and certain among these can attain a measure of abundance, sharing dominance in various combinations with *Nardus* in transitional stands, among which intermediates with *Festuca-Agrostis-Galium* grassland are particularly extensive. Thus, *Festuca ovina* (with some *F. vivipara* at higher altitudes) and *Agrostis capillaris* are constants of the community, and *Anthoxanthum odoratum* is very common, with *Deschampsia flexuosa* an additional constant in the most widely distributed kinds of *Nardus-Galium* grassland. *Agrostis canina* is frequent in some sub-communities, although it has not always been separated from *A. capillaris* in the data, nor often diagnosed to the subspecies, so its exact status here is a little uncertain. *Danthonia decumbens* is only occasional overall, though it becomes more common in certain situations and *Festuca rubra* can likewise occur with modest frequency. Sometimes these other grasses form the basis of a fine and varied turf, preferentially cropped by stock, among the upstanding *Nardus* tussocks; in other cases, they are

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reduced to small patches or sparse tufts of this or that species isolated among the densely-growing dominant though given some shelter from grazing by it. Very occasionally, too, the cover may be varied by scattered tussocks of *Molinia caerulea*, although generally speaking this is a very scarce plant in the community and only in rather particular situations does it become difficult to separate the *Nardus-Galium* grassland from vegetation in which *Molinia* plays an important role.

More problematical from a diagnostic point of view is the occurrence here of *Juncus squarrosus*. Overall, this is a frequent plant in the *Nardus-Galium* grassland and one of the few species able to hold its own against *Nardus*, though it is more common in some sub-communities than others, and even then is very variable in its cover, ranging from sparse to co-dominant. However, it is sometimes hard to distinguish this vegetation from the *Juncus-Festuca* community and indeed certain workers (Birks 1973, Birse & Robertson 1976, Evans *et al.* 1977, Hill & Evans 1978, Birse 1980) have combined stands in which either *Nardus* or *Juncus* is dominant with a similar range of associates into single syntaxa. In fact, although the two vegetation types do grade one into the other in continuous fashion, when the proportions of *Nardus* or *Juncus* have to be relied upon to effect a separation, they are rather different in their overall floristic character and in their habitat preferences.

Also very common, but likewise variable in its abundance, is *Vaccinium myrtillus*, usually present as scattered sprigs and often grazed hard back, and never really bushy and vigorous, but sometimes a little more extensive and giving a grass-heath structure to the vegetation. No other sub-shrubs occur so frequently throughout, although *Calluna vulgaris* is occasionally found and preferentially common in some sub-communities, and there is sometimes a little *Vaccinium vitis-idaea*, *Empetrum nigrum*, *Erica tetralix* or *E. cinerea*, these last three able to show local prominence where this vegetation establishes itself on the thin peat of run-down wet heath or the eroding fringes of blanket mire. *Scirpus cespitosus*, by and large a rare plant in the *Nardus-Galium* grassland, can figure frequently in such situations, too, and it also occurs in stands transitional to more chionophilous vegetation with *Nardus*, like some of that which McVean & Ratcliffe (1962) placed in their *Nardus-Trichophorum* nodum. In general, however, the scarcity of *Carex bigelowii* here, at most occasional and usually of low cover, is a good distinguishing feature between the *Nardus-Galium* grassland and the *Nardus-Carex* community which takes in most of that kind of snow-bed.

Other monocotyledons which occur with some frequency in this vegetation, though generally as scattered individuals, are *Carex pilulifera* and *C. binervis*, with sometimes also *C. nigra*; and, where there is local flushing of the swards with more lime-rich drainage waters, more basiphile sedges like *C. panicea*, *C. pulicaris* and *C. flacca* can become common and quite extensive. *Luzula multiflora* and/or *L. campestris* are also characteristic of some sub-communities, although again there may have been some confusion between these species in the data and care should be taken to assess their respective contributions here (Wiggington & Graham 1981). *L. sylvatica* can sometimes be found, too, but it is typically infrequent and of low cover. Where stands have developed on redistributed peat, *Eriophorum angustifolium* or *E. vaginatum* occur very occasionally and flushed *Nardus-Galium* grassland may have a little *J. effusus*.

Among dicotyledonous herbs, only *Galium saxatile* and *Potentilla erecta* are found with any frequency and, except where there is some flushing, this element of the vegetation is usually very impoverished with just scarce plants of *Polygala serpyllifolia* and *Campanula rotundifolia*. Even modest irrigation, however, can bring considerable enrichment and variety, with mesophytic species such as *Viola riviniana*, *Cerastium fontanum*, *Ranunculus acris*, *Plantago lanceolata* and *Trifolium repens* becoming common, sometimes with more calcicolous plants where the waters are more base-rich.

Bryophyte cover in the *Nardus-Galium* grassland is very variable, though even quite densely tussocky swards usually have some mosses growing among the litter. Pleurocarps are particularly important, with *Rhytidiadelphus squarrosus*, *Hypnum cupressiforme s.l.*, *Hylocomium splendens* and *Pleurozium schreberi* all occurring frequently and sometimes in abundance. There is also quite often some *Dicranum scoparium*, and *Polytrichum commune* is especially characteristic of one sub-community, with *P. formosum* and *P. alpinum* occurring very occasionally too, and *P. juniperinum* on sparse patches of bare ground. *Racomitrium lanuginosum* can also become locally common and abundant in one kind of *Nardus-Galium* grassland and there is very rarely a local abundance of *Sphagnum papillosum*. *Lophocolea bidentata s.l.* and *Ptilidium ciliare* are the most frequent hepatics, but there is occasionally some *Calypogeia muellerana*, *Lophozia ventricosa* and *Barbilophozia floerkii* and local enrichment with more oceanic liverworts is a feature of some stands. Lichens are typically few and scarce but with *Racomitrium* there is often some *Cladonia uncialis* and occasionally a little *Cetraria islandica*.

Sub-communities

Species-poor sub-community: *Nardetum strictae* Smith & Moss 1903, Smith & Rankin 1903, Lewis 1904*a,b*, Moss 1911, Tansley 1939, all *p.p.*; Grass moor Smith 1911 *p.p.*; *Nardus-Deschampsia* grassland Adamson

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1918; *Nardetum sub-alpinum*, species-poor facies McVean & Ratcliffe 1962, Meek 1976, Ferreira 1978, all *p.p.* *Nardus* is almost always the most abundant plant in this sub-community and is usually a clear dominant, although there is frequently some *Deschampsia flexuosa* and this can attain quite high cover, when its flowering shoots often give the vegetation a distinctive silver-purple sheen in early summer. *Festuca ovina*, by contrast, remains very common but is usually of low cover and *Agrostis capillaris* is distinctly patchy in its representation, with *A. canina* much less frequent than in the next sub-community. *Anthoxanthum* is quite often found, though again it is not abundant, and species such as *Danthonia* and *F. rubra* occur only rarely.

Juncus squarrosus is only moderately frequent in this kind of *Nardus-Galium* grassland and usually of low cover, but *Vaccinium myrtillus* has its best representation in the community here, being often found as numerous shoots growing among the grasses, and there is occasionally some *V. vitis-idaea* too, though *Calluna* is very scarce. *Galium saxatile* and *Potentilla erecta* are both very common, and the former can be fairly abundant, and *Carex pilulifera* and *C. binervis* occur quite frequently as scattered plants. *Luzula multiflora* is rare but *L. campestris* is preferential at low frequency and another distinctive feature in some stands is *Alchemilla alpina*.

As often in this community, bryophyte cover is somewhat patchy, but there are generally some of the pleurocarpous mosses growing among the herbage and these can be quite abundant, with *Pleurozium schreberi* and *Hylocomium splendens* especially frequent and showing high cover in some stands, particularly where more vigorous growth of *V. myrtillus* gives a heathy feel to the vegetation.

***Agrostis canina-Polytrichum commune* sub-community:** Marginal *Nardetum* Smith 1918; *Nardetum* Price Evans 1932; *Festuca-Nardus-Juncus squarrosus* Grassland Ratcliffe 1959; *Nardetum sub-alpinum*, species-poor facies McVean & Ratcliffe 1962, Eddy *et al.* 1969 *p.p.*; *Nardus stricta* sociation Edgell 1969; *Nardo-Juncetum squarrosi* Birks 1973 *p.p.*, Evans *et al.* 1977, Hill & Evans 1978. *Nardus* usually remains the most abundant plant here, but it is not so strongly dominant as in the Species-poor sub-community, and mixtures of *F. ovina* and *A. capillaris*, with some *D. flexuosa*, *Anthoxanthum* and, strongly preferential to this vegetation, *Agrostis canina*, often make a quite substantial contribution to the cover. *V. myrtillus* is fairly common, too, and, where it is a little more abundant, along with scattered *C. pilulifera* and *C. binervis* and wefts of the bulky pleurocarpous mosses, there is a floristic gradation to richer stands of the last sub-community. Very often, however, there is some *J. squarrosus* here, together with *Luzula multiflora*, occasional *Carex nigra* and *C. bigelowii* and, among the bryophytes, *Polytrichum commune* is strongly preferential, along with frequent *Ptilidium ciliare* and occasional *Barbilophozia floerkii* and *Lophocolea bidentata s.l.* Where the rush is more abundant, as in some of the stands described from Moor House by Eddy *et al.* (1969), the vegetation grades to the *Juncus-Festuca* community. *Galium saxatile* and *Potentilla erecta* are very frequent throughout, but other dicotyledons are rare.

***Carex panicea-Viola riviniana* sub-community:** *Nardetum sub-alpinum*, species-rich facies McVean & Ratcliffe 1962; Species-rich *Juncus-Nardus* nodum Eddy *et al.* 1969; *Nardo-Juncetum squarrosi* Birks 1973 *p.p.*; *Junco squarrosi-Festucetum tenuifoliae* Birse & Robertson 1976 *emend.* Birse 1980 *p.p.*; *Cirsium palustre-Nardus stricta* Community Birse 1980. Although *Nardus* is almost always the most abundant plant in these swards, its cover is somewhat variable and *F. ovina* is fairly often a co-dominant, with some *A. capillaris* and *Anthoxanthum* and occasional *Agrostis canina*. *D. flexuosa*, by contrast, is here very scarce and, unusually for the *Nardus-Galium* grassland, there is hardly ever any *V. myrtillus*. Frequent *J. squarrosus* and *L. multiflora* maintain a floristic continuity with the previous sub-community, but the really striking feature of this vegetation is the range of more mesophytic and basiphile plants, some of them characteristic of moister soils, that find a place. Among the grasses, for example, *Festuca rubra* and *Holcus lanatus* add occasional variety, and there is quite often some *Carex panicea*, *C. pulicaris*, *C. demissa* and *C. flacca* rather than the more usual *C. pilulifera* and *C. binervis*. Along with frequent *Galium saxatile* and *Potentilla erecta*, plants such as *Viola riviniana*, *Cerastium fontanum*, *Plantago lanceolata*, *Trifolium repens* and *Leontodon autumnalis* occur fairly commonly and give the vegetation the stamp of a damp mesotrophic grassland or, with occasional *Juncus effusus*, *Cirsium palustre* and *Achillea ptarmica*, a grassy poor fen. In other cases, the occasional presence of species like *Selaginella* and *Thymus praecox* with more of the calcicolous small sedges brings the herbage close to a base-rich flush. Bryophyte cover is rather variable but *Rhytidiadelphus squarrosus* and *Hylocomium splendens* are the commonest mosses with *Thuidium tamariscinum* preferentially frequent and *Calliergon cuspidatum* occasional, and where these are abundant, the vegetation takes in some of what McVean & Ratcliffe (1962) called *Hypno-Caricetum alpinum*. *Lophocolea bidentata s.l.* is the only common hepatic.

***Calluna vulgaris-Danthonia decumbens* sub-community:** *Nardo-Galietum saxatilis* Shimwell 1968*a*. *Nardus* is generally dominant in this sub-community, though not

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overwhelmingly so, and there is often quite abundant *F. ovina* and *A. capillaris*, with some *Anthoxanthum* and occasional *D. flexuosa* and, preferentially frequent here, *Danthonia decumbens*. *V. myrtillus* is common but it is generally *Calluna* that gives a distinctive character to this kind of *Nardus-Galium* grassland and, in some stands, it is quite abundant, though typically grazed down to short sprigs. Much more locally, *Erica cinerea* or *E. tetralix* can be found at moderately high cover. *G. saxatile* and *P. erecta* remain very frequent and there is occasional *C. pilulifera* and *C. binervis*, but other herbaceous associates are few. *Hypnum cupressiforme s.l.*, *Dicranum scoparium* and *Pleurozium* are the commonest bryophytes, although *Pseudoscleropodium purum* is preferential at low frequency.

***Racomitrium lanuginosum* sub-community:** *Nardus-Trichophorum* nodum McVean & Ratcliffe 1962 *p.p.*; *Nardus* is usually dominant here and all other grasses, particularly *Agrostis capillaris* and *Anthoxanthum*, are reduced in frequency and cover: generally there is just a little *F. ovina* with occasional *D. flexuosa* and *Agrostis canina* between the tussocks. *J. squarrosus* is fairly common, but more distinctive in this vegetation is the frequency of *Scirpus cespitosus*, and this is often quite abundant, sometimes co-dominant with the *Nardus*. Both *V. myrtillus* and *Calluna* occur commonly and each can have moderately high cover; occasionally, too, there is some *Empetrum nigrum*, *Erica tetralix* or *E. cinerea*, and local abundance of these can add to the heathy appearance of the vegetation, though characteristically the sward is short. *Galium saxatile* tends to be rather patchy in its representation but *Potentilla erecta* remains frequent and there is occasional *Huperzia selago* and *Narthecium ossifragum* along with scattered plants of *C. pilulifera*, *C. binervis* and *C. nigra*. The other striking feature of this sub-community is the common occurrence of *Racomitrium lanuginosum*, sometimes in considerable quantity, and though there can be a little *Rhytidiadelphus loreus* along with *Hypnum cupressiforme s.l.* pleurocarps are generally sparse. Occasional *Diplophyllum albicans*, *Scapania gracilis* and *Pleurozia purpurea* can give a somewhat oceanic look to the vegetation and, unusually among *Nardus-Galium* grasslands, there are quite often some lichens here, most frequently *Cladonia uncialis* with occasional *Cetraria islandica*.

Habitat

The *Nardus-Galium* grassland is typical of moist, peaty mineral soils, usually base-poor and infertile, over the higher hill slopes of the cool, wet north and west of Britain. It is a secondary vegetation type which contributes extensively to our poorer-quality upland grazings and, though climate and soils exert a strong influence on the general floristic features of the community and its internal variation, its spread owes much to particular kinds of pastoral treatment.

Even more so than the *Festuca-Agrostis-Galium* grassland, this is a vegetation type of the rainy and cool uplands. Swards with some *Nardus* are not unknown in the warmer and drier lowlands of Britain – the species makes a modest contribution there to a variety of grasslands and heaths – but the abundance of the plant in this kind of vegetation is strongly concentrated within the 1200 mm isohyet (*Climatological Atlas* 1952), where there are more than 160 wet days yr^{-1} (Ratcliffe 1968), and where the mean annual maximum isotherm is 26 °C or less (Conolly & Dahl 1970), a zone which takes in much of the South-West Peninsula, Wales, northern England and Scotland. Through these regions, then, conditions are generally cloudy and humid, with very small potential water deficits, less than 25 mm across most of the range of the community (Page 1982), and though there is a strong tendency to leaching, even over parent materials that are not wholly lime-deficient, soils are kept moist for much of the year. Very much as in the *Festuca-Agrostis-Galium* grassland, therefore, these swards take much of their general floristic character from the occurrence of plants like *Anthoxanthum*, *Agrostis canina*, *Deschampsia flexuosa*, *Danthonia*, *Carex binervis* and *C. pilulifera*, along with the more universally distributed *Festuca ovina*, *Agrostis capillaris*, *Galium saxatile* and *Potentilla erecta*; from the abundance of pleurocarpous mosses like *Rhytidiadelphus squarrosus*, *Hylocomium splendens* and *Pleurozium*; and from the vigorous growth of these associates, where the dominant allows, helping to exclude the ephemerals and light-demanding chamaephytes so characteristic of the open Thero-Airion swards of the drought-prone acid soils in the lowlands.

The floristic and environmental overlap between the *Nardus-Galium* and *Festuca-Agrostis-Galium* grasslands is thus very considerable: both are essentially submontane Nardo-Galion communities and indeed it is likely that the former occupies some ground which could carry the latter and has been derived there from it. However, although both can extend at their upper extreme to 800 m or so, the altitudinal distributions of the two vegetation types are rather different, the *Festuca-Agrostis-Galium* grassland being typically found between 150 and 500 m, the *Nardus-Galium* grassland being concentrated from 300 to 700 m, with a mean altitude more than 200 m above that of the other community. There is little obvious direct effect of the cooler and more humid conditions prevailing over these higher slopes on the flora of the *Nardus-Galium* grassland apart from the encouragement of the generally montane *V. myrtillus*: Arctic-Alpines like *Carex bigelowii*, *V. uliginosum* and *Empetrum nigrum* ssp. *herm-*

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aphroditum still play an insignificant role here and only beyond 700 m or so, where mean annual maxima often fall below 22 °C (Conolly & Dahl 1970), do they become important with *Nardus* in the *Nardus-Carex* community.

The more evident effects of climate on the *Nardus-Galium* grassland are indirect ones felt through pedogenesis, because the association of this vegetation with higher ground is essentially a reflection of its preference for moister acid soils, frequently podzolised and often gleyed, with substantial accumulations of surface mor. The *Festuca-Agrostis-Galium* grassland does extend some little way on to such profiles in the *Vaccinium-Deschampsia* sub-community, which is floristically transitional to the *Nardus-Galium* grassland, but it is by and large a vegetation type of more free-draining brown podzolics or podzols proper, with moder or but a thin humose topsoil. Beneath the *Nardus-Galium* grassland, by contrast, the commonest profiles are of the stagnopodzolic or stagnohumic gley type (Avery 1980), in which there is often more than 10 cm, sometimes up to 30 cm, of peaty topsoil, with varying degrees of leaching and gleying below, according to the particular character of the parent material and the drainage conditions of the ground (Tansley 1939, McVean & Ratcliffe 1962, King 1962, King & Nicholson 1964, Birse & Robertson 1976, Hill & Evans 1978, Birse 1980, 1984). Such soils are very widely distributed throughout the uplands, occurring extensively as intergrades on the gentle transitions between steeper, shedding slopes, which provide a typical location for the *Festuca-Agrostis-Galium* grassland, and the summit plateaus above, with their deep ombrogenous peats from which the *Nardus-Galium* grassland is characteristically excluded except where the material has been eroded and redistributed over a mineral base (Smith 1918, Pearsall 1968). But they are also commonly found over gentle receiving slopes throughout the altitudinal range and in transitions to flushes where the ground is back-gleyed.

The more poorly drained among these soils are frequently derived from impervious bedrocks such as the Ordovician and Silurian shales that are so extensive beneath the community through the Southern Uplands and West Wales, and the Carboniferous shales that provide an important substrate in the Pennines. The softness of such argillaceous rocks also means that they tend to weather to more subdued landscapes on to which run-off is channelled from the upstanding hill slopes around and over which drainage is fairly sluggish. The extensive deposition of heavy-textured drift, such as glacial till, over gentler slopes through the sub-montane zone exacerbates such stagnation and, by insulating the vegetation from the underlying bedrocks, such superficials can carry the *Nardus-Galium* grassland on to ground which would be otherwise too sharply drained. But the community also occurs widely on a variety of more coarse-textured and initially pervious parent materials, both bedrocks and drift, where a measure of drainage impedence has resulted from the formation of a thin iron pan with long-continued leaching. In other cases, profiles can be kept suitably moist by irrigation and, among tracts of dry soils, the *Nardus-Galium* grassland is quite often an indicator of modest flushing: it can even extend on to free-draining alluvium along stream sides (McVean & Ratcliffe 1962, Welch 1967). Except very locally, the ground waters are lime-poor and, although the community can be found over calcareous rocks, the strong tendency to leaching means that, in most cases, the superficial pH is between 3.5 and 5 (McVean & Ratcliffe 1962, King 1962, King & Nicholson 1964). The generally heavy rainfall at these higher altitudes is also important in encouraging the accumulation of the thick layers of mor, even over quite steep and more freely draining ground, and in guarding against any strong tendency to droughting.

It is this combination of edaphic conditions that is so conducive to the vigour of *Nardus* in this vegetation: first and foremost, it is a plant that favours a humose topsoil moist for much of the year but in an oxidising state in summer, and a mineral base, generally strongly leached, preferably highly impoverished and often gleyed (Pearsall 1950, Chadwick 1960). In such circumstances it is able to outcompete its potential rivals, particularly where, as is often the case here, treatments have put these other plants at an additional disadvantage. Among the associates which are more typical of this community than of the *Festuca-Agrostis-Galium* grassland, *V. myrtillus*, *D. flexuosa* and *Pleurozium*, *J. squarrosus*, *L. multiflora* and *P. commune* are also favoured by the soil conditions that prevail here, the first three where the profiles tend to be more free-draining, the last three where they are distinctly peaty and moister. Variations in the proportions of these species account for much of the difference between the two widely-distributed kinds of *Nardus-Galium* grassland, the Typical and the *Agrostis-Polytrichum* sub-communities and a general edaphic contrast may underlie these distinctions: certainly the latter sub-community is more common at higher altitudes – its mean is some 75 m above that of the former type – and in places where redistributed peat provides a moist and highly humose substrate, as around some of the summits in the Southern Uplands.

There is strong edaphic continuity between the conditions characteristic of these two types of *Nardus-Galium* grassland and the *Calluna-Danthonia* and *Racomitrium* sub-communities, where the soils are likewise generally base-poor and impoverished. The *Calluna-Danthonia* swards essentially continue the floristic trends of Typical *Nardus-Galium* grassland into some of the drier and warmer upland fringes where the community occurs. Its mean altitude is more than 100 m less than that of most stands of the community and it is the usual form of *Nardus-Galium* grassland to be found on podzolic soils on Exmoor, through southern Wales, the Peak District and the Pennine fringes, where rainfall is usually less than 1600 mm yr^{-1} (*Climatological Atlas* 1952) with often fewer than 180 wet days yr^{-1} (Ratcliffe 1968), and where mean annual maxima are generally over 25 °C (Conolly & Dahl 1970). Here, peat-loving plants tend to make their minimal contribution and the vegetation grades into sub-montane heathy grassland.

Towards the opposite extreme, the *Racomitrium* sub-community takes the *Nardus-Galium* grassland into some of the wettest and coolest situations where generally suitable soils are to be found. Through the range of this kind of vegetation, the annual rainfall is usually well over 1600 mm (*Climatological Atlas* 1952) with more than 200 wet days yr^{-1} (Ratcliffe 1968) and mean annual maxima of less than 23 °C (Conolly & Dahl 1970). In some places, a sunless northerly or easterly aspect provides a local enhancement of these cool, moist conditions with some prolongation of snow-lie. With the shelter that this offers, the *Racomitrium* sub-community can extend to well over 600 m in the central Highlands, grading to certain kinds of chionophilous *Nardus-Carex* vegetation (McVean & Ratcliffe 1962). Other stands occur at lower altitudes than this, over slopes that are quite exposed, but where the general climatic conditions are more equable, such that the cover resembles a grassy moss-heath: extensive tracts of such vegetation occur on North Harris (Ratcliffe 1977) and Shetland. The cool oceanic climate is reflected in the *Racomitrium* sub-community in the frequency of *R. lanuginosum*, *Cladonia uncialis* and the occasional Atlantic bryophytes, with *Scirpus cespitosus*, *Molinia* and *Empetrum nigrum* providing continuity with the run-down wet heaths so extensive through those parts of Britain where thin ombrogenous peats have been eroded and their vegetation burned and grazed.

The very different swards of the *Carex-Viola* sub-community extend the *Nardus-Galium* grassland on to soils that are considerably more base-rich than usual, where the ground is irrigated by run-off from calcareous rocks. Its distribution thus tends to be local, though it can be widespread where such substrates make an important contribution to the landscape, as with the more lime-rich of the Dalradian metasediments between Breadalbane and Clova, and especially over the flanks of Ben Lawers (McVean & Ratcliffe 1962). More isolated stands have been recorded from similar rocks on Shetland (Birse 1980), over Tertiary basalts on Skye (Birks 1973) and where there is flushing from limy partings among Silurian shales in the Southern Uplands (Ferreira 1978) and from Carboniferous Limestone in the Pennines (Welch 1967). The soils under the *Carex-Viola* sub-community tend to have little raw humus and they can sometimes be distinctly silty where fine material has been washed downslope or deposited alongside flooding streams. The tendency to gleying varies but it is often pronounced and irrigation keeps the pH nearer 6 than 5, the typical upper limit for other kinds of *Nardus-Carex* grassland. Under such conditions, species such as *J. squarrosus* and *L. multiflora* can persist but *Nardus* loses some of its competitive edge and the more strongly calcifugous among the associates fade in importance to be replaced by the characteristic diversity of mildly basiphile and mesophytic plants.

Throughout its range, over this variety of soil types and substrates, the *Nardus-Galium* grassland is typically an element in the open hill grazings that occupy the lower and middle slopes beyond the limits of enclosure and, among the patchworks of vegetation types available to stock there, it is among the least valuable for sustaining the kinds of animals favoured these days (Stapledon 1937, Fenton 1953). For one thing, much more so than with the *Festuca-Agrostis-Galium* grassland, the community prefers soils that are not only for the most part base-poor, but also highly oligotrophic, so the amounts of lime and major nutrients in the herbage are relatively low (e.g. Pearsall 1968). More obviously, there is the characteristic prevalence of *Nardus* in the swards and, though this grass is of similar digestibility to other fine-leaved species (Thomas & Fairburn 1956, Hodgson & Grant 1981), it has a much higher proportion of fibrous tissue in its wiry foliage (Burr & Turner 1933, Pearsall 1968), so it represents a very unrewarding bite. Indeed, most stock, particularly sheep, are reluctant to graze it when offered a choice and, though the community may receive a little more attention than usual in the winter months when herbage is in generally short supply (Hunter 1954, 1962), it can suffer grazing intensities less than half those experienced by the *Festuca-Agrostis-Galium* grassland (Boulet 1939, Hunter 1962).

Cattle, which were the more important animals throughout the uplands until the eighteenth century, are not quite so choosy as sheep and have been reported to turn to *Nardus* sooner, though they do not graze it very closely (Nicholson *et al.* 1970, Grant *et al.* 1985), while ponies, not often pastured in the uplands now but still locally important, can nip out the growing centres of the tussocks and discard the tough leaf bases (Havinden & Wilkinson 1970). Significantly, where there has remained some diversity among the stock, as on Dartmoor where both cattle and ponies are still pastured along with sheep, the *Nardus-Galium* grassland is noticeably uncommon among the open grazings, despite the presence of eminently suitable soils (Ward *et al.* 1972*a*). In Scotland, too, Fenton (1936, 1937) and

Wilson (1936) noted that the contribution of *Nardus-Galium* grassland declined where Galloway cattle were put out to graze. Then, there is the striking description from Roberts (1959) of the avid way in which all-winter wethers will attack *Nardus* (and *J. squarrosus*) just as late-winter leaf initiation is occurring, biting out the new growth and leaving the old tussock surrounds to be whipped away by the wind.

Such evidence, together with historical accounts of what has happened to hill grazings over the last few centuries, has led to the convincing suggestion that the widespread entrenchment of the *Nardus-Galium* grassland among *Festuca-Agrostis-Galium* and other better-quality swards has been strongly favoured by the switch from cattle to sheep as the predominant upland grazing stock and, more recently, from wethers to the more choosy breeding ewes (Fenton 1937, Roberts 1959). But the differences in the timing of the more intense bouts of grazing between the older and newer pastoral systems may be just as important as the variations in selectivity between the animals (King & Nicholson 1964, Grant *et al.* 1985) and it is also very clear that the success of *Nardus* in spreading through particular tracts of pasture is strongly influenced by interaction between treatments and soil conditions. Generally speaking, the species does best where uncontrolled but selective grazing has been applied over long periods to swards on moist, peaty and infertile ground. Where it is less able to compete for edaphic reasons, the response of *Nardus* to a favourable pastoral regime will be muted; conversely, on soils of intermediate suitability it is most readily affected by treatment changes (Ratcliffe 1959*a*). Then, as a general background to such responses, there may be a tendency for the *Nardus-Galium* grassland to mark the progressive deterioration of upland grazings with centuries of exploitation since clearance (Ratcliffe 1959*a*, King & Nicholson 1964).

Zonation and succession

The *Nardus-Galium* grassland occurs widely through the uplands of northern and western Britain in zonations and mosaics with a variety of other grasslands, heaths and mires, where the major influences on the vegetation patterns are soil differences and treatments. Regional climatic variations across the range of the community affect the particular components of these patchworks and local climatic differences mediate transitions to windswept moss-heath and snow-beds. In most situations, however, the *Nardus-Galium* grassland is an anthropogenic vegetation type, derived by the burning and grazing of cleared land in the forest zone. Although relaxation of pasturing might allow a ready reversion to heath in many places, the run-down of ground long occupied by the community may hinder any succession to forest at lower altitudes.

Some of the clearest edaphically-related zonations involving the *Nardus-Galium* grassland can be seen where the moist, peaty soils that it favours occur as intergrades between more sharply draining podzols and rankers on steeper, shedding slopes and thicker peats kept moist by heavy rainfall or locally impeded drainage over flatter ground. Quite commonly, such patterns find clear expression in an altitudinal banding with a zone of *Nardus-Galium* grassland occupying the gentler ground on transitions between the steeper hillsides below and the summit plateaus above, but more complex patterns can be seen over stepped topography or more broken slopes. The zonation over the drier podzols is very often to the *Festuca-Agrostis-Galium* grassland and, over graded transitions on higher hills, the *Vaccinium-Deschampsia* sub-community of that vegetation, which has occasional *Nardus*, can pass almost imperceptibly into Species-poor *Nardus-Galium* grassland. In other cases, sharper topographical changes from slope to plateau, or scarp to dip, can show a more abrupt zonation of these vegetation types: these sometimes mark geological shifts from resistant pervious bedrocks to softer, impervious ones, as over grit/shale alternations, while elsewhere the deposition of heavy drift sharpens up drainage differences by enhancing impedence over gentler slopes. Then, the sudden change in the abundance of *Nardus* may provide a much better indication of the boundaries between the communities, the belts and patches of the *Nardus-Galium* grassland showing up especially clearly in winter, although there is still often considerable qualitative continuity among the associates in the swards. Patterns of these kinds are very widespread through the British uplands, and well illustrated in the account of the Moffat Hills (Smith 1918) and, in more fragmentary fashion, in maps of the Carneddau (Ratcliffe 1959*a*) and Cader Idris (Edgell 1969). They have been clearly described too from the southern Pennines, although here the swards of the steeper, better-drained ground tend to be of the *Deschampsia flexuosa* type (Adamson 1918), while in the warm oceanic south-west of England such *Nardus-Galium* grassland as does occur is often found in association with the *Agrostis curtisii* grassland (e.g. Ward *et al.* 1972*a*).

In the other direction in edaphic transitions of this kind, the *Nardus-Galium* grassland often passes to some kind of bog or related vegetation on ombrogenous peat that has accumulated over summit plateaus or high-level terraces. Ultimately, it is blanket mire that usually terminates such sequences, with the *Calluna-Eriophorum* bog occurring over the flatter summits of the Grampians, the higher ground in the Southern Uplands and down the Pennines, the more oceanic *Scirpus-Eriophorum* bog being found in association with the community in more westerly parts of Scotland, in

Wales and the south-west of England. And sometimes the *Nardus-Galium* grassland can give way abruptly to such vegetation, with little floristic continuity, where the peat mantle becomes suddenly thicker. Often, however, there is an intervening zone with a more gentle transition between the extremes, either over the gradually thickening humose topsoil that eventually passes to deep intact peat, or over redistributed peat eroded from the blanket bog fringe above and washed down over the slopes, this latter a widespread and extensive feature of many upland areas now. In such zonations, the *Agrostis-Polytrichum* sub-community is often the commonest form of *Nardus-Galium* grassland and this can grade to Ericion wet heath over thicker peats, the *Juncus-Dicranum* sub-community of the *Ericetum tetralicis* figuring widely in these patterns in the east-central Highlands, the *Vaccinium* sub-community of the more oceanic *Scirpus-Erica* wet heath being commoner through the Southern Uplands, Wales and the South-West Peninsula. Moving into such vegetation, the grass cover usually becomes patchy, with *Scirpus cespitosus* and sub-shrubs such as *V. myrtillus*, *Calluna*, *Empetrum nigrum* and *Erica tetralix* increasing in abundance, and Sphagna like *S. capillifolium*, *S. compactum*, *S. subnitens* and *S. tenellum* appearing. In other cases, *Dicranum scoparium*, *Racomtrium lanuginosum*, pleurocarpous mosses and various larger lichens can become prominent in these transitions and, over exposed fringes of eroding blanket mire around the western seaboard of Scotland, the *Racomitrium* sub-community of the *Nardus-Galium* grassland can play a locally important part in gradations to wet heath (Ratcliffe 1977). Another very common plant over these intermediate zones of wet but fairly thin peat is *Juncus squarrosus*, which occurs widely in all proportions with *Nardus*, either in intimate mixtures or in complicated patchy mosaics with one or the other species dominant. In this scheme, a distinct *Juncus-Festuca* grassland subsumes most of the vegetation of this kind in which *J. squarrosus* is clearly the more abundant plant (cf. Ratcliffe 1959*a*, Birks 1973, Birse & Robertson 1976, Birse 1980), but gradations between this and *Nardus-Galium* grassland, particularly the *Agrostis-Polytrichum* and *Carex-Viola* sub-communities, can be complex and virtually continuous (Ratcliffe 1959*a*, Welch 1967).

The *Nardus-Galium* grassland can also be found as a transitional community where free-draining soils give way to gleys maintained by irrigation from springs or seepage lines, and indeed in regions with very poor rocks such as the quartzites which prevail in parts of the western Highlands, such habitats provide a local but important site for this vegetation among suites of oligotrophic heaths. Much more widely, however, the *Nardus-Galium* grassland occurs on peaty gleys around soligenous flushes, the *Agrostis-Polytrichum* sub-community often marking out a gradation from drier swards to calcifuge Caricion nigrae vegetation like the *Carex echinata-Sphagnum* mire, the *Carex nigra-Nardus* sub-community of which has frequent *Nardus*, *Anthoxanthum*, *Festuca ovina*, *Agrostis canina* ssp. *canina*, *Juncus squarrosus*, *Luzula multiflora* and *Polytrichum commune*, as well as *Carex echinata*, *C. nigra*, *C. demissa*, *Viola palustris* and various Sphagna, most notably *S. recurvum*, *S. auriculatum* and *S. palustre*. Where the irrigating waters are somewhat more base-rich, as occurs on slopes receiving run-off or seepage from calcareous rocks or drift, the *Carex-Viola* sub-community usually occurs in these transitional situations, either marking out flushed zones within tracts of more calcifuge Species-poor *Nardus-Galium* grassland or forming a surround to strongly basiphile mires like the *Pinguiculo-Caricetum* or, at higher altitudes, the *Carici-Saxifragetum*. Well-developed flushes with this kind of vegetation are usually clearly marked off from their context by their richness in calcicolous small sedges, dicotyledons and bryophytes, but transitional and fragmentary stands can be harder to delineate from the neighbouring swards, especially where the ground is much trampled by stock searching for a nourishing bite. Patterns of this kind are a striking feature of some of the Breadalbane Mountains, as over the slopes of Ben Lawers (Ratcliffe 1977) where McVean & Ratcliffe (1962) grouped some of the more strongly flushed transitions with *Nardus* in a distinct *Hypno-Caricetum*.

Towards higher altitudes, it becomes difficult to distinguish between the *Nardus-Galium* grassland and the *Nardus-Carex* vegetation which has been largely unaffected by the burning and grazing prevalent over lower ground and which often has a distinctly chionophilous character. The two communities come closest on north- and east-facing slopes where shade maintains a particularly cool and moist atmosphere and where some prolongation of snow-lie provides shelter from the biting winds and an additional source of irrigating waters in late spring. Here, the *Racomitrium* sub-community, often with a local abundance of *Scirpus cespitosus*, can provide a surround to Typical *Nardus-Carex* snow-bed vegetation, a pattern well seen in some of the great corries on Beinn Eighe and certain of the Grampian mountains (Ratcliffe 1977).

Almost everywhere else, treatments have interacted with soils and climate to complicate the kinds of vegetation patterns described above. First, there is the general feature that, where pastoral exploitation of hill grazings by choosy stock has been long and heavy, the *Nardus-Galium* grassland tends to occupy more of the ground in such sequences than would be the case if edaphic factors had exerted a greater control on its abundance, the community becoming deeply entrenched over the most suitable profiles and being at a strong competitive advantage over better-quality swards on soils of a transitional character. Second, over ground of intermediate wetness and impoverishment, there can be seen all manner of fine variation in the composition and structure of the swards where grazing exerts its maximal influence on zonations between the *Nardus-Galium* grassland and other communities like the *Festuca-Agrostis-Galium* grassland, from sharply-delimited mosaics of close-cropped runnels between *Nardus* tussocks to much more ill-defined gradations between short and ranker swards. There is probably some measure of successional play in such patterning, whereby the boundaries can be sharpened up or allowed to become less clear with variations in grazing intensity, but because selective cropping tends to confirm the hold of *Nardus* in the swards, it is doubtful whether increased stocking with choosy animals can ever push back the limits of the *Nardus-Galium* grassland without imposing unacceptable pressure on the better-quality swards. Less selective stock, such as cattle, ponies and wethers, are probably better for this purpose, the first having the advantage of a heavier tread and more concentrated manuring, which helps break up the rank herbage and raise the fertility of the ground. Milton (1940) showed that controlled heavy grazing, with such dunging and trampling, could reduce the abundance of both *Nardus* and *J. squarrosus* in grasslands such as these, though in dense *Nardus-Galium* swards it is unknown whether the required closeness of grazing can be achieved without the stock suffering nutritional penalties (Nicholson *et al.* 1970, Grant *et al.* 1985).

Little information is available on the detailed fate of *Nardus-Galium* grassland from which grazing has been withdrawn apart from the enclosure experiments at Moor House in the northern Pennines (Welch & Rawes 1964, Rawes 1981) and even here the changes are still in train after 20 years or so of protection from sheep and the results somewhat equivocal. But the most obvious indications are that, where *Nardus* has a strong hold in the swards over highly suitable soils, it declines little, or even increases its abundance, with enclosure, whereas if it is a relatively minor component over profiles that are not so moist and peaty, it declines, being overwhelmed in this case by plants such as *Deschampsia flexuosa* and *Carex bigelowii*. Similar observations were made by Ratcliffe (1959*a*) on unplanted patches or failed areas within forestry enclosures in Snowdonia, where mixed *Nardus*, *Festuca* and *Agrostis* swards became dominated by *D. flexuosa*, *A. capillaris*, *V. myrtillus* and *Calluna*. And so it seems likely that, where *Nardus* is not unduly abundant, and perhaps at some competitive disadvantage once grazing is withdrawn, it is plants that can root in the mat of accumulating litter that are best able to thrive and subdue it. The likely successor to such changes through most of the altitudinal range of the *Nardus-Galium* grassland would be some sort of *Vaccinium-Deschampsia* heath, and indeed this vegetation is frequently found among these swards, sharing many species with them and often grading imperceptibly with changes in dominance that are probably often under biotic control (Ratcliffe 1959*a*, McVean & Ratcliffe 1962, King & Nicholson 1964). At lower altitudes, heather can become important in such patterns, with the *Nardus-Galium* grassland occurring among *Calluna-Vaccinium* heath, particularly the *Galium-Festuca* sub-community, or, through the southern Pennines, the *Calluna-Deschampsia* heath, or, over higher ground in the oceanic south-west of Britain, the *Ulex gallii-Agrostis curtisii* heath.

It seems highly likely that in some regions sub-shrub vegetation of these kinds, rather than other grasslands, were the historical precursors to the *Nardus-Galium* swards. Certainly, Ratcliffe (1959*a*) and McVean & Ratcliffe (1962) adduced abundant evidence that repeated burning together with heavy grazing had converted sub-montane heather communities to bilberry heath, *Nardus-Galium* and *Festuca-Agrostis-Galium* grasslands through much of the Southern Uplands, northern England and Wales, and was continuing to do so; and they supposed the same to be true of parts of the Highlands, particularly in the drier south-east Grampian region. And King (1960), from observations in parts of the Southern Uplands, suggested that the development of *Nardus*-dominance might be an intermittent but cumulative process related to the cyclic, but gradually less successful, regrowth of heather with repeated burning, or perhaps just after many generations of natural growth and ageing. It is, however, often impossible to tell whether particular tracts of *Nardus-Galium* grassland have developed in this secondary fashion or more directly from cleared forest and, in recent times, the latter process may have been the more widespread (McVean & Ratcliffe 1962).

What is clear is that reversion of the *Nardus-Galium* grassland to woodland with a relaxation of grazing is often problematic. Quite apart from the rarity of seed-parents through much of the sub-montane zone, the thick, litter-choked herbage and peaty mat present a very uncongenial rooting medium for likely invaders such as species of birch and pine whose fruits, though wind-transportable over considerable distances, have but small food reserves to sustain root growth down to a mineral base; and, even then, this is a very impoverished substrate. The development of some surface heterogeneity subsequent to the spread and eventual death of sub-shrubs perhaps presents a better prospect: in the forestry enclosures which Ratcliffe (1959*a*) described, seedlings of *Sorbus aucuparia* were occasionally found among the heath. Theoretically, the kinds of forest that would be expected to grow on the better soils at present occupied by the *Nardus-Galium* grassland would be the *Quercus-Betula-Dicranum* woodland with, at higher altitudes, perhaps also the *Pinus-Hylocomium* woodland; but whether there is ever any real likelihood of a full succession to such vegetation, without some intervention such as burning off of the herbage, is unknown. The wetter and more impoverished soils are even less likely to support ready tree growth although, at lower altitudes, a bout of heavy cattle-grazing, with much trampling and manuring, might be a suitable preparation for enclosure and the development of rushy vegetation with spontaneous willow-dominated stands of *Betula-Molinia* woodland.

Distribution

The *Nardus-Galium* grassland occurs widely through the north and west of Britain, though it is scarce through the western Highlands, and much more locally abundant where there has been a history of suitable treatments. The Species-poor and *Agrostis-Polytrichum* sub-communities are both common and widespread on suitable substrates over higher ground throughout the range, the *Calluna-Danthonia* sub-community more occasional at lower altitudes. The *Carex-Viola* type is much more sporadic, though locally abundant over calcareous substrates as through Breadalbane. The *Racomitrium* sub-community is also of sparse distribution, though an extensive feature of some sites around the Atlantic seaboard of Scotland.

Affinities

Nardus grasslands were early recognised as making a distinctive and important contribution to the hill grazings of Britain and a variety of *Nardeta* separated from *Molinia* and *Festuca-Agrostis* swards on the basis of the dominance of the mat-grass (Smith & Moss 1903, Smith & Rankin 1903, Lewis 1904*a*,*b*, Moss 1911, Smith 1918, Price Evans 1932, Tansley 1939, Edgell 1969). In fact, distinction from grassy *Molinia-Potentilla* mire or *Molinia*-rich *Scirpus-Erica* wet heath is rarely a problem, but *Nardus*-dominance has to remain an important criterion for separating the *Nardus-Galium* grassland from communities like the *Festuca-Agrostis-Galium* and *Deschampsia flexuosa* grasslands with which it shares many Nardetalia herbs and bryophytes (King 1962, King & Nicholson 1964).

McVean & Ratcliffe (1962) were the first to provide a clearer definition of our more anthropogenic *Nardus* vegetation in their separation of *Nardetum sub-alpinum* from a variety of other communities of higher altitudes often with some influence from snow-lie, and this distinction remains in this scheme in the recognition of a separate *Nardus-Carex* community, where an increase in species such as *C. bigelowii*, *Cetraria islandica*, *Kiaeria starkei* and *Dicranum fuscescens* and the demise of most of the grasses apart from *Nardus* puts the vegetation firmly among the chionophilous Deschampsieto-Myrtilletalia communities (Dahl 1956). McVean & Ratcliffe (1962) also gave the first indication of the existence of more and less calcifuge kinds of sub-montane *Nardus* vegetation in their recognition of species-poor and species-rich facies. This variation is encompassed here in the characterisation, alongside the Species-poor, *Agrostis-Polytrichum* and *Calluna-Danthonia* sub-communities (which considerably expand McVean & Ratcliffe's species-poor facies in the light of further sampling) of the more basiphile *Carex-Viola* type, a transition to Caricion davallianae vegetation which parallels variation in the *Festuca-Agrostis-Galium* swards. In fact, the *Carex-Viola* sub-community is considerably broader than what McVean & Ratcliffe (1962) recognised as the species-rich *Nardetum*, taking in some of their flushed *Hypno-Caricetum*, and the nearest approach which *Nardus* grasslands make to poor-fen vegetation (Birse 1980).

This scheme also follows McVean & Ratcliffe (1962) in separating the anthropogenic *Nardus* grasslands included in this community from sub-alpine swards in which *Juncus squarrosus* is the dominant. Certainly, the *Juncus-Festuca* and *Nardus-Galium* grasslands show considerable floristic overlap and complex mosaics in which these two species show patchy dominance against a more or less uniform background of associates are of widespread occurrence. However, though a number of authors have diagnosed single vegetation types in which both species can have a prominent role (Ratcliffe 1959*a*, Birks 1973, Birse & Robertson 1976, Evans *et al.* 1977, Hill & Evans 1978, Birse 1980, 1984), the overall floristic and environmental affinities of the plants are rather different, and it makes sense to retain a separate community in which *J. squarrosus* is the usual dominant, with only locally abundant *Nardus* and occasional *Agrostis capillaris*, *Anthoxanthum*, *P. erecta* and *G. saxatile*. In the *Nardus-Galium* grassland, the *Agrostis-Polytrichum* sub-community represents a gradation to such vegetation, which has close floristic and ecological affinities with Ericion wet heath and Erico-Sphagnion blanket mire.

The grassier swards with Nardus, and varying amounts of *J. squarrosus*, that are included in the *Nardus-Galium* grassland clearly belong in the Nardo-Galion alliance (now often termed the Violion caninae following an earlier definition by Schwickerath 1944). But Continental equivalents of the more impoverished *Nardus* pastures characteristic of much of the British uplands are hard to find. Towards the more montane extreme, some stands come close to the various sub-alpine *Nardeta* described from Norway by Nordhagen (1928, 1943), but even secondary swards there have frequent records for such montane and boreal plants as *Omalotheca norvegica*, *Salix lapponum* and *Trientalis* *europaea*. Rather more similar are the swards included in such associations as the *Juncetum squarrosi* (where *J. squarrosus* is in fact neither invariably present nor always abundant), described from Norway (Nordhagen 1922) and France (Stieperaere 1978), and the *Nardo-Caricetum binervis*, originally diagnosed from Ireland (Braun-Blanquet & Tüxen 1952) and since sampled along the Atlantic seaboard of France (Stieperaere 1978). Such vegetation types most closely resemble the *Calluna-Danthonia* sub-community of the *Nardus-Galium* grassland, though they can also have records for species like *Carum verticillatum*, *Wahlenbergia hederacea* and *Scorzonera humilis*, which are rare or local members of Junco-Molinion and related vegetation in Britain. Stieperaere (1978) placed these communities in the Juncion squarrosi (Oberdorfer 1957, Passarge 1964), an alliance of moister Nardo-Galion type swards, retaining the Violion caninae for more xeric vegetation with *Nardus*.

Floristic table U5

	a	b	c	d	e	5
Nardus stricta	V (4–10)	V (4–10)	V (1–8)	V (1–6)	V (1–10)	V (1–10)
Galium saxatile	V (1–6)	V (1–6)	IV (1–6)	V (1–4)	III (1–6)	V (1–6)
Potentilla erecta	IV (1–4)	IV (1–4)	V (1–4)	V (1–4)	V (1–4)	IV (1–4)
Festuca ovina	IV (1–6)	V (1–8)	IV (1–6)	IV (4–8)	III (1–4)	IV (1–8)
Agrostis capillaris	III (1–4)	IV (1–4)	V (1–4)	IV (1–6)	II (1–4)	IV (1–6)
Rhytidiadelphus squarrosus	IV (1–6)	IV (1–6)	V (1–3)	III (1–6)	I (1–3)	IV (1–6)
Deschampsia flexuosa	V (1–6)	V (1–8)	I (1)	II (1–6)	III (1–6)	III (1–8)
Pleurozium schreberi	IV (1–6)	IV (1–6)	I (1–3)	III (1–6)		III (1–6)
Vaccinium vitis-idaea	II (1–4)	I (1–3)		I (1–3)	I (1–3)	I (1–4)
Luzula campestris	II (1–4)	I (1)		I (1)		I (1–4)
Alchemilla alpina	II (1–6)	I (1)		I (1–4)		I (1–6)
Luzula multiflora	I (1–4)	IV (1–3)	IV (1–3)	I (1–3)	I (1)	II (1–4)
Agrostis canina	I (1–4)	IV (1–6)	II (1–4)	I (1–3)	III (1–4)	II (1–6)
Polytrichum commune	II (1–4)	IV (1–4)	I (1–3)	II (1–9)	I (1–4)	II (1–9)
Ptilidium ciliare	I (1–3)	III (1–3)	I (1–3)	I (1–3)	I (1)	II (1–3)
Barbilophozia floerkii	I (1–3)	II (1–3)	I (1–3)		I (1–3)	I (1–3)
Carex bigelowii	I (1–7)	II (1–7)		I (1)	I (1–3)	I (1–7)
Campylopus paradoxus	I (1–6)	II (1–4)		I (1–4)	I (1–3)	I (1–6)
Plagiothecium undulatum	I (1–3)	II (1–3)		I (1)	I (1)	I (1–3)
Carex panicea	I (1–4)	I (1–3)	III (1–4)	I (1–4)	II (1–4)	II (1–4)
Viola riviniana	I (1–3)	I (1–3)	III (1–4)	I (1–4)	I (1)	I (1–4)
Lophocolea bidentata s.l.	I (1)	II (1–3)	III (1–3)		I (1–3)	I (1–3)
Cerastium fontanum	I (1–3)	I (1–3)	III (1–3)	I (1)		I (1–3)
Ranunculus acris	I (1–3)		III (1–4)	I (1)		I (1–4)
Thuidium tamariscinum	I (1–4)	I (1–3)	III (1–4)			I (1–4)
Festuca rubra	I (1–6)	I (1–4)	II (1–4)	I (1–4)	I (1)	I (1–6)
Polygala serpyllifolia	I (1–3)	I (1–3)	II (1–3)	I (1–3)	I (1)	I (1–3)
Juncus effusus	I (1–4)	I (1–3)	II (1–3)	I (1–4)		I (1–4)
Carex demissa	I (1–4)	I (1)	II (1–3)		I (1–3)	I (1–4)
Plantago lanceolata	I (1–3)		II (1–4)	I (1)		I (1–4)
Leontodon autumnalis	I (1–3)		II (1–3)	I (1)		I (1–3)

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Floristic table U5 (*cont.*)

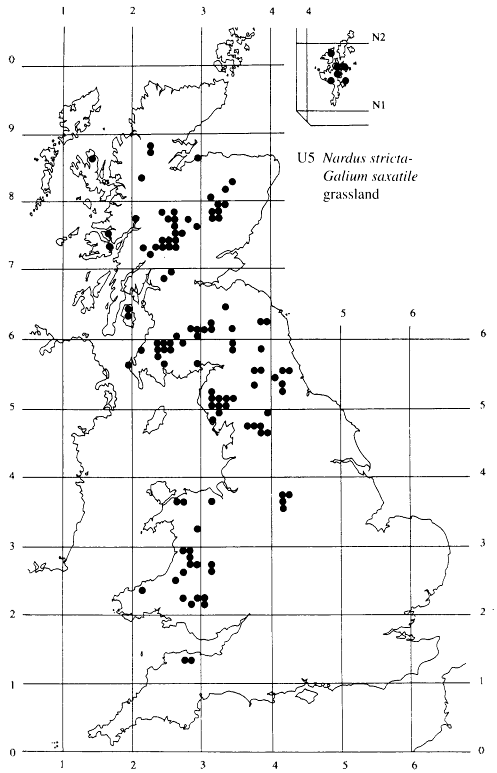
	a	b
Calliergon cuspidatum	I (1–3)	
Trifolium repens	I (1–3)	
Equisetum palustre		I (1–3)
Cirsium palustre		
Selaginella selaginoides		
Carex pulicaris		
Calluna vulgaris	I (1–8)	I (1–4)
Danthonia decumbens	I (1–4)	I (1–3)
Pseudoscleropodium purum	I (1–6)	I (1–3)
Erica tetralix	I (1)	I (1)
Scirpus cespitosus	I (1–6)	I (1–4)
Racomitrium lanuginosum	I (1–4)	I (1–8)
Cladonia uncialis	I (1–3)	I (1–4)
Molinia caerulea	I (1–6)	I (1–6)
Rhytidiadelphus loreus	I (1–4)	I (1–4)
Diplophyllum albicans	I (1–3)	I (1–3)
Narthecium ossifragum	I (1–4)	I (1–3)
Empetrum nigrum	I (1–6)	I (1–6)
Huperzia selago	I (1–3)	I (1–4)
Cetraria islandica	I (1–3)	I (1–3)
Scapania gracilis		
Pleurozia purpurea		
Juncus squarrosus	III (1–6)	IV (1–8)
Vaccinium myrtillus	IV (1–8)	III (1–6)
Anthoxanthum odoratum	IV (1–6)	III (1–4)
Hypnum cupressiforme	III (1–6)	IV (1–4)
Hylocomium splendens	III (1–4)	II (1–4)
Carex binervis	II (1–4)	II (1–4)
Carex pilulifera	II (1–6)	II (1–4)
Dicranum scoparium	II (1–6)	II (1–4)
Carex nigra	I (1–6)	II (1–3)

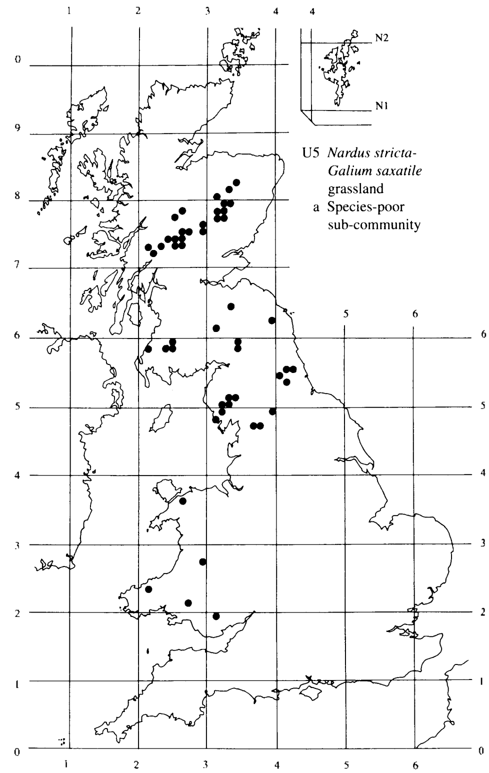
c	d	e	5
II (1–4)			I (1–4)
II (1–4)			I (1–4)
II (1–3)			I (1–3)
II (1–3)	I (4)		I (1–4)
II (1–3)			I (1–3)
II (1–4)			I (1–4)
II (1–4)	IV (1–8)	IV (1–8)	II (1–8)
II (1–3)	IV (1–4)	II (1–3)	II (1–4)
I (1–4)	II (1–4)		I (1–6)
	II (1–6)	I (1–4)	I (1–6)
I (1)	I (1–4)	IV (1–8)	I (1–8)
I (1)	I (1–6)	IV (1–10)	I (1–10)
	I (1–3)	III (1–4)	I (1–4)
I (1–3)	I (1–6)	II (1–3)	I (1–6)
I (1–3)	I (1)	II (1–3)	I (1–4)
	I (1)	II (1–6)	I (1–6)
	I (1)	II (1–4)	I (1–4)
	I (1–6)	II (1–6)	I (1–6)
	I (1–3)	II (1–3)	I (1–4)
	I (1–4)	II (1–2)	I (1–4)
I (1)		II (1–3)	I (1–3)
		II (2–4)	I (2–4)
IV (1–6)	II (1–4)	III (1–4)	III (1–8)
I (1–3)	IV (1–6)	III (1–6)	III (1–8)
V (1–4)	III (1–4)	I (1–3)	III (1–6)
II (1–3)	II (1–4)	III (1–6)	III (1–6)
III (1–6)	I (1–4)	I (1–4)	III (1–6)
I (1–4)	II (1–4)	II (1–3)	II (1–4)
I (1–3)	II (1–4)	II (1–4)	II (1–6)
I (1–3)	II (1–6)	II (1–3)	II (1–6)
II (1–4)	I (1–3)	II (1–3)	II (1–6)

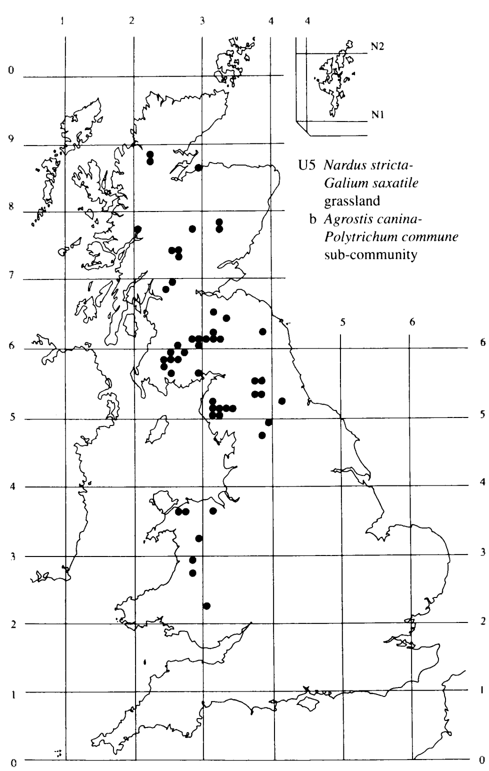
Luzula sylvatica	I (1–6)	I (1–4)
Campanula rotundifolia	I (1–4)	I (1–3)
Deschampsia cespitosa	I (1–6)	I (1–6)
Polytrichum alpinum	I (1–4)	I (1–4)
Polytrichum formosum	I (1–5)	I (1–3)
Eriophorum angustifolium	I (1–6)	I (1–4)
Calypogeia muellerana	I (1–3)	I (1–3)
Eriophorum vaginatum	I (1–3)	I (1–6)
Aulacomnium palustre		I (1–6)
Lophozia ventricosa	I (1–3)	I (1–3)
Pohlia nutans	I (1–3)	I (1–3)
Blechnum spicant	I (1–4)	I (1–3)
Polytrichum juniperinum	I (1–4)	I (1)
Anemone nemorosa	I (1–3)	I (1)
Dicranella heteromalla	I (1)	I (1–3)
Erica cinerea	I (1)	
Sphagnum papillosum		I (1–5)
Number of samples	104	137
Number of species/sample	20 (11–32)	20 (9–36)
Herb height (cm)	16 (3–40)	20 (8–38)
Herb cover (%)	93 (50–100)	99 (85–100)
Ground layer height (mm)	24 (10–50)	21 (10–40)
Ground layer cover (%)	28 (1–80)	9 (0–30)
Altitude (m)	522 (142–860)	596 (165–976)
Slope (°)	17 (0–50)	12 (0–45)
Soil pH	4.0 (3.3–5.8)	4.0 (3.4–5.0)

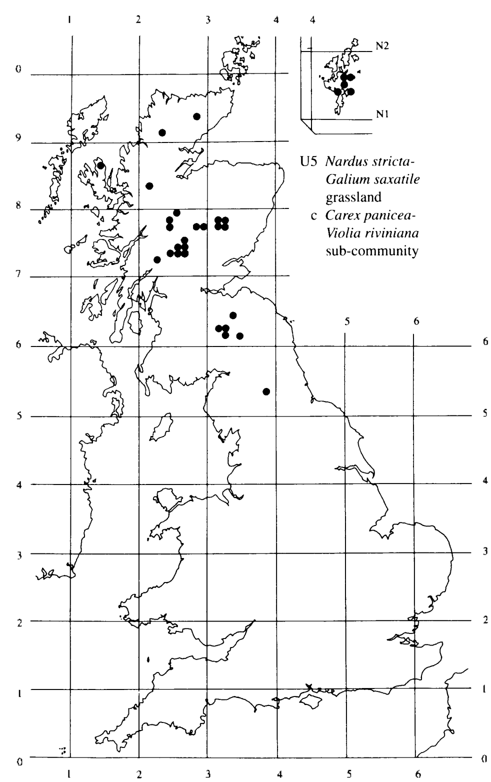
a Species-poor sub-community
b *Agrostis canina-Polytrichum commune* sub-community
c *Carex panicea-Viola riviniana* sub-community
d *Calluna vulgaris-Danthonia decumbens* sub-community
e *Racomitrium lanuginosum* sub-community
5 *Nardus stricta-Galium saxatile* grassland (total)

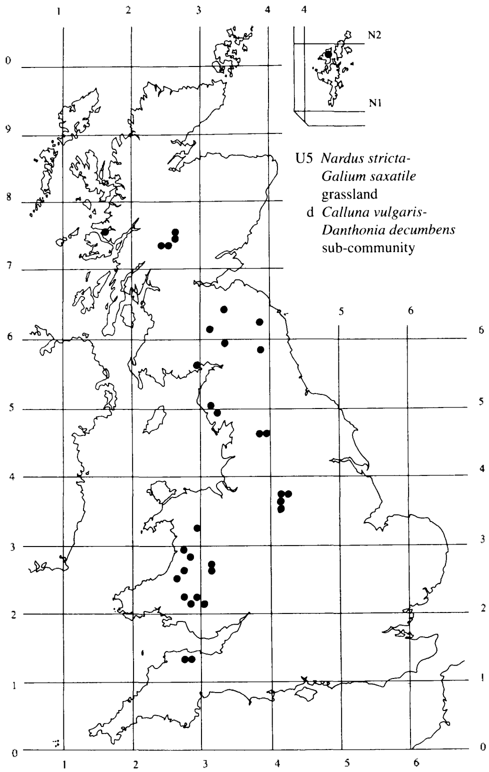
I (1–3)	I (1)		I (1–6)
I (1–3)	I (1–3)		I (1–4)
I (1–6)	I (1)		I (1–6)
I (1)	I (1–3)		I (1–4)
I (1–3)		I (1–3)	I (1–5)
	I (1)	I (1–3)	I (1–6)
	I (1–3)	I (1–3)	I (1–3)
	I (1–3)	I (1–3)	I (1–6)
I (1–4)	I (1)	I (1–3)	I (1–6)
	I (1)		I (1–3)
	I (1)		I (1–3)
	I (1–4)		I (1–4)
	I (1–4)		I (1–4)
	I (1)		I (1–3)
	I (1)		I (1–3)
	I (1–4)	I (1–6)	I (1–6)
I (1–9)		I (1–6)	I (1–9)
37	42	35	355
28 (15–42)	20 (6–33)	22 (11–39)	21 (6–42)
18 (14–23)	13 (2–47)	12 (6–21)	16 (2–47)
97 (80–100)	91 (20–100)	82 (20–100)	95 (20–100)
15 (10–20)	16 (10–30)	25 (10–50)	22 (10–50)
32 (20–90)	38 (0–100)	34 (20–60)	24 (0–100)
517 (306–838)	401 (173–762)	581 (290–895)	541 (142–976)
8 (0–28)	23 (0–75)	15 (0–39)	15 (0–75)
5.9 (5.6–6.1)	4.6 (3.5–6.2)	4.4 (3.6–5.2)	4.3 (3.3–5.2)

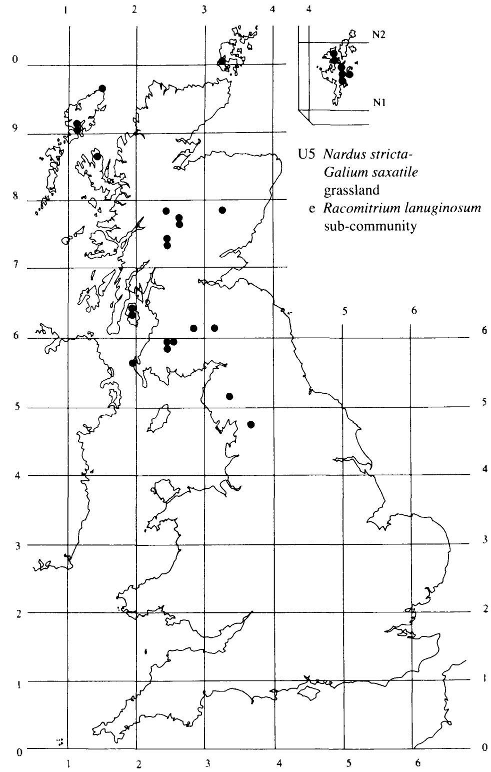

U5 Nardus stricta-
Galium saxatile
grassland


U5 Nardus stricta-
Galium saxatile
grassland
a Species-poor
sub-community


U5 Nardus stricta-
Galium saxatile
grassland
b Agrostis canina-
Polytrichum commune
sub-community


U5 Nardus stricta-
Galium saxatile
grassland
c Carex panicea-
Violia riviniana
sub-community





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