U4
Festuca ovina-Agrostis capillaris-Galium saxatile grassland

Synonymy
Siliceous grassland Smith 1900*a,b*, 1905, Crampton 1911, Tansley 1911, all *p.p.*; *Festuca-Agrostis* grassland Tansley 1939, Ratcliffe 1959*a*, King 1962, Pearsall 1968; *Festuceto-Agrostidetum* Balme 1953; *Viola lutea* grass-heath Balme 1954 *p.p.*; *Festuca-Nardus* grassland Ratcliffe 1959*a*; Species-poor *Agrosto-Festucetum* McVean & Ratcliffe 1962, Birks 1973, Meek 1976, Evans *et al.* 1977, Ferreira 1978; *Agrostis-Festuca* sociation Edgell 1969; *Agrostis-Festuca-Nardus* sociation Edgell 1969; *Festucetum* Eddy *et al.* 1969; *Achilleo-Festucetum tenuifoliae* Birse & Robertson 1976; *Galium saxatile-Poa pratensis* community Birse & Robertson 1976; *Agrosto-Festucetum* Hill & Evans 1978 *p.p.*; *Trifolio-Agrosto-Festucetum* Hill & Evans 1978; *Anthoxantho-Festucetum rubrae* Page 1980; *Junco squarrosi-Festucetum tenuifoliae* Birse & Robertson 1976 *emend.* Birse 1980 *p.p.*; *Festuca ovina-Anthoxanthum odoratum-Trifolium repens-Agrostis tenuis* & *Festuca ovina-Nardus stricta* noda Hughes & Huntley 1986.

Constant species
Agrostis capillaris, *Anthoxanthum odoratum*, *Festuca ovina*, *Galium saxatile*, *Potentilla erecta*.

Physiognomy
The *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland is characteristically dominated by grass mixtures in which *Festuca ovina*, *Agrostis capillaris* and *Anthoxanthum odoratum* are the most consistent and generally the most abundant components. *F. tenuifolia* has sometimes been specifically distinguished from *F. ovina sensu stricto* in the data (Birse & Robertson 1976, Birse 1980, Graham 1988), but as yet there is no accurate indication of the relative importance of the two taxa in the community. *F. vivipara* has also been recorded in some higher-altitude stands but is otherwise rare. *F. rubra* is not so common throughout as *F. ovina* but, in certain situations, it can exceed it in frequency and cover. *Agrostis canina* occurs occasionally, with ssp. *canina* being particularly well represented on damper ground.

Typically, these grasses occur intimately mixed in swards that are short, sometimes a little rough and tussocky, but often close-cropped into a tight, fine-textured turf. No other grasses have the same general importance in the community as a whole, though a number are found as occasionals throughout, notably *Danthonia decumbens*, and some others can attain local prominence, in certain cases giving a distinctly coarser look to the herbage. *Nardus stricta*, for example, is usually a low-frequency associate here, though it can get a firmer hold and become very obvious in autumn when its tussocks stand out straw-yellow against the mid-green background; but, even then, the plants are typically scattered and *Nardus* never shows the uncompromising dominance in this community that is so characteristic of much *Nardus-Galium* grassland. Likewise, *Deschampsia flexuosa*, which can become fairly frequent in some kinds of *Festuca-Agrostis-Galium* grassland and grow quite tussocky, is usually of no more than modest abundance among the dominants. In other stands, *D. cespitosa* is preferentially common, though with nothing like the consistency and vigour that it shows in related grasslands of flushed and snow-bound slopes.

Another group of grasses that can become prominent in these swards in certain circumstances includes more mesophytic species like *Holcus lanatus*, *Dactylis glomerata*, *Poa pratensis* and *Cynosurus cristatus*, with occasional *Lolium perenne* providing more obvious indication of the agricultural improvement that has often occurred in enclosed stands, and a clear floristic transition to more productive Cynosurion pastures. Where there is some amelioration of base-poverty, plants like *Avenula pratensis* and *Briza media* can make an appearance, though this is an exceptional and usually local occurrence. Towards the opposite edaphic extreme, *Holcus mollis* can show striking abundance over res-

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tricted areas, often with a suspicion of having been inherited from cleared woodland.

On soils which are a little peaty, there can also be some *Molinia caerulea* in this community, but overall this species is uncommon and hardly ever of even moderate abundance, so distinctions from grassy *Molinia-Potentilla* mire are usually fairly clear. In contrast to that vegetation, too, and to the *Juncus-Galium* and *Holco-Juncetum* rush-pastures, big rushes like *Juncus acutiflorus* and *J. effusus* are very infrequent here, though the grassland can be found in close association with these communities and may regress to them where stands have been derived by draining and then neglected. Hard-grazed and ill-drained tracts of the *Festuca-Agrostis-Galium* grassland can also have some *Juncus squarrosus*. Characteristically, however, the most common associated monocotyledons are *Luzula campestris*, locally replaced by *L. multiflora*, and a number of sedges, *Carex pilulifera* and *C. binervis* being the most common, *C. panicea*, *C. echinata*, *C. nigra*, *C. bigelowii* and *C. caryophyllea* occurring at low frequency in particular sub-communities. Each of these may show some degree of abundance in the sward but they do not generally disrupt its fine-grained character.

The dicotyledon flora of the *Festuca-Agrostis-Galium* grassland is generally not very numerous or diverse, and in comparison with the *Festuca-Agrostis-Thymus* grassland, the community mostly deserves the epithet 'species-poor' (McVean & Ratcliffe 1962), though there are some particular situations where the swards can present a pleasing richness among the associates. Throughout, however, only *Galium saxatile* and *Potentilla erecta* are constant and, in many stands, these are accompanied by just occasional *Viola riviniana*, *Rumex acetosa*, *Ranunculus acris*, *Veronica officinalis*, *Polygala serpyllifolia* and *Euphrasia officinalis* agg. (including *E. micrantha*, *E. confusa* and *E. brevipila*), the plants often being grazed down to diminutive rosettes or prostrate patches. Less frequent overall but quite characteristic is *Viola lutea* and there are sometimes records for *Veronica chamaedrys*, *Oxalis acetosella*, *Conopodium majus*, *Ranunculus repens* and *Viola palustris*, with coarse weeds like *Cirsium vulgare* and *C. arvense* sometimes marking out ill-managed stands on better soils. *Thymus praecox* can also be found here and exceptionally it may be accompanied by stricter calcicoles like *Sanguisorba minor* and *Helianthemum nummularium* but, as among the grasses, distinctions from the *Festuca-Agrostis-Thymus* grassland are usually clear. Similarly, stands on coastal cliff tops may have occasional records for *Plantago maritima*, *P. coronopus*, *Armeria maritima* or *Scilla verna* but a consistent maritime component is lacking.

More ill-defined among this element of the vegetation is the separation from neutral swards because, under certain conditions, species such as *Trifolium repens*, *Achillea millefolium*, *Cerastium fontanum*, *Campanula rotundifolia*, *Lotus corniculatus* and *Galium verum* can become fairly common, and some of these swards are further enriched by *Succisa pratensis*, *Lathyrus montanus* and *Stachys betonica*.

Quite often, too, the *Festuca-Agrostis-Galium* grassland is found in intimate association with heath vegetation and mosaics with and gradations to such communities are widespread. Indeed, there is occasionally a little *Calluna vulgaris* or *Vaccinium myrtillus* scattered through these swards, more locally some *Empetrum nigrum* ssp. *nigrum*, and sometimes such representation becomes a little more frequent. The cover of such plants, though, is characteristically of low order, indeed any shoots of heather and bilberry are often grazed right back, and transitional stands can usually be separated on whether grasses or sub-shrubs have overall dominance. A similar criterion can generally be applied to distinguish those stands of the *Festuca-Agrostis-Galium* grassland which have some *Pteridium aquilinum* from the *Pteridium-Galium* community. Bracken is typically infrequent through the grassland as defined here and usually of low abundance, but it very commonly gets a hold on the kinds of soils favoured by these swards and can readily spread into them so, again, transitions are common.

In the closed and often dense turf typical here bryophytes are not usually very abundant. *Rhytidiadelphus squarrosus* is the most characteristic species and its slender shoots are frequently found growing with low cover among the herbage. Then, there is quite commonly some *Hypnum cupressiforme s.l.*, *Hylocomium splendens*, *Dicranum scoparium* and *Pseudoscleropodium purum*, again usually fairly sparse, but sometimes thickening up locally into small patches. More unevenly distributed among the sub-communities but occasionally prominent are *Pleurozium schreberi*, *Rhytidiadelphus loreus*, *Thuidium tamariscinum* and *Racomitrium lanuginosum*, with *Polytrichum commune*, *P. alpinum*, *Rhytidiadelphus triquetrus* and *Mnium hornum* occurring at low frequency throughout the grassland.

Sub-communities

Typical sub-community: *Festuca-Agrostis* grassland Ratcliffe 1959*a*; Species-poor *Agrosto-Festucetum* McVean & Ratcliffe 1962, Birks 1973, Meek 1976, Evans *et al.* 1977, Hill & Evans 1978, Ferreira 1978; Type C *Festuca ovina/Agrostis* spp. grassland King 1962; *Festuca-Agrostis* type 5 grassland King & Nicholson 1964; *Agrostis-Festuca* sociation Edgell 1969; *Achilleo-Festucetum tenuifoliae* Birse & Robertson 1976; *Festuca ovina-Anthoxanthum odoratum* nodum Hughes & Huntley 1986. In this, the most widespread and common type of *Festuca-Agrostis-*

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Galium grassland, dominance is generally shared by various mixtures of *F. ovina* (less frequently *F. rubra*), *Agrostis capillaris* (occasionally *A. canina*) and *Anthoxanthum*. *Danthonia* is quite common but usually of low cover and *Nardus* and *Deschampsia flexuosa* are only occasional and very rarely of any abundance. *Holcus lanatus* is infrequent and other mesophytic grasses are hardly ever found. *Luzula campestris* and *Carex pilulifera* are very common and slightly preferential to this sub-community.

Among the dicotyledons, only *Potentilla erecta* and *Galium saxatile* are constant but the latter can be locally quite abundant. There is also fairly frequent *Viola riviniana*, *Plantago lanceolata*, *Veronica officinalis* and *Achillea millefolium* with occasional *Lotus corniculatus*, *Galium verum*, *Trifolium repens* and *Cerastium fontanum*, though all of these are usually present as scattered individuals. *Calluna* occurs at low frequency, often grazed hard back to little sprigs but *Vaccinium myrtillus* is uncommon.

Bryophytes are fairly numerous and together they can have quite high cover with *R. squarrosus* most common and locally abundant. *Hylocomium splendens* and *Pleurozium* are a little less frequent but also sometimes quite conspicuous, *Pseudoscleropodium*, *D. scoparium* and *H. cupressiforme* fairly common but usually not abundant.

***Holcus lanatus-Trifolium repens* sub-community:** Types D & F *Festuca ovina/Agrostis* spp. grassland King 1962; Type E *Agrostis tenuis/Festuca* spp. grassland King 1962; *Festuca-Agrostis* type 9 grassland King & Nicholson 1964; *Agrostis-Festuca* type 10 grassland King & Nicholson 1964; *Galium saxatile-Poa pratensis* community Birse & Robertson 1976 *p.p.*; *Trifolio-Agrosto-Festucetum* Evans *et al.* 1977; *Agrosto-Festucetum*, *Trifolium repens* facies Hill & Evans 1978; *Anthoxantho-Festucetum rubrae* Page 1980; *Trifolium repens-Agrostis tenuis* nodum Hughes & Huntley 1986. *F. rubra* often replaces *F. ovina* here as a co-dominant with *A. capillaris* and *Anthoxanthum* and there is characteristically some *Holcus lanatus* in the sward, not usually with more than modest cover but often abundant enough to give a somewhat different look to the vegetation, particularly where, as is quite frequently the case, it is accompanied by small amounts of *Dactylis*, *Poa pratensis* and *Cynosurus*. Some stands, particularly in pastures taken in around the upland fringes and improved a little, can have some *Lolium perenne* or occasional *Phleum pratense* or *Alopecurus pratensis*. By contrast, *Deschampsia flexuosa* and *Nardus* are typically very scarce and even *Danthonia* tends to be rather infrequent and patchy.

This trend towards a more mesophytic composition is reflected among the dicotyledonous associates. Both *Galium saxatile* and *Potentilla erecta* are rather less common than usual in this sub-community whereas species such as *Trifolium repens*, *Achillea millefolium* and *Cerastium fontanum*, which are only occasional in Typical *Festuca-Agrostis-Galium* grassland, become strongly preferential. Then, community occasionals such as *Plantago lanceolata*, *Rumex acetosa* and *Viola riviniana* are joined by *Galium verum*, *Lotus corniculatus*, *Prunella vulgaris*, *Taraxacum officinale* agg., *Trifolium pratense* and *Bellis perennis*, all of these at fairly low frequency and typically of sparse occurrence. Sub-shrubs are rare.

Bryophytes usually make some contribution to the sward but more calcifuge species are scarce, with *R. squarrosus* and *Pseudoscleropodium* being the most frequent.

***Lathyrus montanus-Stachys betonica* sub-community:** *Festuceto-Agrostidetum* Zone III Balme 1953. The usual dominants here are *F. ovina* (occasionally with some *F. rubra*) and *A. capillaris*, with *Anthoxanthum* very common but generally subordinate in cover. Mesophytic grasses are typically no more than occasional but a distinctive feature is the fairly frequent occurrence of *Avenula pratensis*, *Koeleria macrantha* and *Briza media*. *Danthonia* is quite common, but *Deschampsia flexuosa* and *Nardus* are characteristically scarce, though they can spread into this vegetation, the former in particular becoming locally prominent in succession to more uniformly calcifuge swards. *Luzula campestris* is very common and *Carex caryophyllea* is preferential at low frequency, with occasional records in damper stands for *C. panicea* and *C. pulicaris*.

Galium saxatile is a little patchier than in Typical *Festuca-Agrostis-Galium* grassland, but most of the other general community dicotyledons remain fairly common, with scattered plants of *Potentilla erecta*, *Viola riviniana*, *Rumex acetosa*, *Plantago lanceolata*, *Achillea millefolium*, *Ranunculus acris* and *Veronica officinalis*. *Campanula rotundifolia*, *Lotus corniculatus* and *Gallium verum* are recorded more frequently here than in other sub-communities, but the most striking preferentials are *Lathyrus montanus*, *Stachys betonica* and *Succisa pratensis*. In some areas, as on drift-derived soils over the Derbyshire Limestone, *Viola lutea* is also strongly diagnostic of this kind of grassland, and there, too, calcicolous herbs such as *Sanguisorba minor* and *Helianthemum nummularium* can occasionally be found in these swards, with *Anemone nemorosa* on shadier aspects. *Calluna* is sometimes recorded but *V. myrtillus* is the commoner invading sub-shrub, though its occasional plants are usually kept severely in check by grazing.

Bryophytes are generally not abundant, with just sparse shoots of *R. squarrosus*, *H. cupressiforme*, *D. scoparium*, *P. schreberi* and *Pseudoscleropodium*.

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***Luzula multiflora-Rhytidiadelphus loreus* sub-community:** Type I *Agrostis tenuis/Deschampsia caespitosa* grassland King 1962; *Deschampsia-Festuca-Agrostis* type 8 grassland King & Nicholson 1964; *Agrosto-Festucetum, Deschampsia cespitosa* facies Hill & Evans 1978. *F. ovina* is quite often replaced by *F. rubra* and/or *F. vivipara* in this sub-community, with *A. canina* ssp. *canina* frequently joining *A. capillaris* and *Anthoxanthum*. Various mixtures of these usually dominate, although *Deschampsia cespitosa* is preferentially common here and it can have modest abundance. *Nardus* is also frequent, with *D. flexuosa* occasional, but *Danthonia* and mesophytic grasses are generally scarce. Very characteristically, *L. multiflora* largely replaces *L. campestris* and there are sometimes records for *Carex panicea* and *C. echinata* as well as for *C. pilulifera* and *C. binervis*. *Luzula sylvatica* can be locally common and there is occasionally a little *Juncus squarrosus*.

Both *G. saxatile* and *P. erecta* remain very frequent but other dicotyledons are not numerous: *Viola riviniana* is common but, apart from this, there is usually just occasional *Cerastium fontanum*, *Ranunculus acris* and *Succisa pratensis*. No preferentials occur among this element of the flora although *Blechnum spicant* is recorded a little more often than usual.

Bryophyte cover is rather variable, but along with frequent *Rhytidiadelphus squarrosus*, *Hylocomium splendens* and *Hypnum cupressiforme* and occasional *Pleurozium schreberi* and *Pseudoscleropodium purum*, there is preferentially common *Rhytidiadelphus loreus* and *Thuidium tamariscinum*, and a number of these can occur as locally abundant tufts among the herbage.

***Vaccinium myrtillus-Deschampsia flexuosa* sub-community:** *Festuceto-Agrostidetum* Zone IV Balme 1953; *Festuca-Nardus* grassland Ratcliffe 1959*a*; Types B & G *Festuca ovina/Deschampsia flexuosa* (*Nardus stricta*) grassland King 1962; *Festuca-Deschampsia* (*Nardus*) type 3 grassland King & Nicholson 1964; *Agrostis-Festuca-Nardus* sociation Edgell 1969; *Festucetum* Eddy *et al.* 1969; *Junco squarrosi-Festucetum tenuifoliae* Birse & Robertson 1976 *emend.* Birse 1980; *Festuca ovina-Nardus stricta* nodum Hughes & Huntley 1986. *F. ovina* (occasionally *F. rubra*) and *A. capillaris* generally dominate here, but *Nardus* is very frequent and it can be quite abundant, with *D. flexuosa* also common and locally of high cover. *Anthoxanthum* is somewhat less frequent than usual, indeed often distinctly patchy and not generally abundant. *Agrostis canina*, typically ssp. *montana*, and *Danthonia* are occasional, and there is sometimes a little *Deschampsia cespitosa*. Mesophytic grasses are very scarce. *Luzula campestris* is quite common and *Carex binervis* and *C. pilulifera* are sometimes joined by small amounts of *C. bigelowii* and occasional *Juncus squarrosus*.

Of all the kinds of *Festuca-Agrostis-Galium* grassland, this has the poorest herbaceous dicotyledon flora and, apart from scattered plants of *Potentilla erecta* and *Galium saxatile*, there is often just very occasional *Viola riviniana*. But sub-shrubs are commoner here than elsewhere, with fairly frequent *Calluna* and constant *V. myrtillus*, each sometimes of moderately high cover but typically grazed back to short shoots. *Pteridium* is also a little more frequent here than in other sub-communities.

Among the bryophytes, *Pleurozium schreberi* is a constant associate of *Rhytidiadelphus squarrosus* and *Dicranum scoparium* and, along with occasional *Hypnum cupressiforme* and *Hylocomium splendens*, there is sometimes a little *Polytrichum commune* and *Racomitrium lanuginosum*. The pleurocarps in particular can become quite abundant in this vegetation.

Habitat

The *Festuca-Agrostis-Galium* grassland is the most extensive kind of pasture on better-drained, more base-poor mineral soils through the cool and wet sub-montane zone of north-west Britain. Climate and soils play a significant part in determining the floristic character of the vegetation and variation within it, but this is everywhere a plagioclimax community which takes much of its distinctive stamp from the influence of grazing stock. It is a grassland of major agricultural importance, making up the bulk of the better-quality rough grazing over steeper unenclosed slopes at moderate altitudes through the upland fringes, as well as including somewhat more improved grazings taken in and upgraded towards the limits of enclosure.

The community can be considered as the sub-montane counterpart of the *Festuca-Agrostis-Rumex* grassland, being largely excluded from otherwise suitable soils in the warmer and drier lowlands of Britain by their susceptibility to summer parching. Stands transitional between the two vegetation types can be found in The Weald, where the rainfall is substantially greater than over much of south-east England, but by and large, the *Festuca-Agrostis-Galium* grassland is confined to those parts of the country where precipitation exceeds 800 mm yr^{-1} (*Climatological Atlas* 1952) and where the mean annual maximum temperature is less than 27 °C (Conolly & Dahl 1970). Through this zone, which takes in much of the South-West Peninsula, all of Wales and the Marches, and most of northern England and Scotland, these climatic features combine to keep the potential water deficit small, less than 50 mm across most of the range of the community (Page 1982), and even the more free-draining profiles can be maintained in a moist state for much of the year.

This shift to cooler, wetter conditions is marked among these calcifugous grasslands by a number of physiognomic and floristic responses. First, there is a change from the open, tussocky turf characteristic of the

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Festuca-Agrostis-Rumex grassland, where the growth of the grasses is held in check, to the closed sward seen here, with its vigorous herbage and general absence of *Rumex acetosella* and light-demanding chamaephytes and of ephemerals able to capitalise upon gaps in the cover. Then, though *Agrostis capillaris* and *Festuca ovina* still commonly make up much of the grassy ground in this community, there is a marked increase in the frequency of *Anthoxanthum*, *F. rubra* and *Danthonia*, and species such as *Potentilla erecta* and *Galium saxatile* are often joined by *Luzula campestris*, *Viola riviniana*, *Carex pilulifera* and *C. binervis*, and the bryophytes *Rhytidiadelphus squarrosus*, *Hylocomium splendens* and *Pleurozium schreberi*, all of them plants which fare less well on the droughty, base-poor soils of the south-east. In the sub-montane zone, on the other hand, they thrive together in the *Festuca-Agrostis-Galium* grassland right up on to shedding slopes of steep angle: the community is commonly found on hills and valley sides of 10–25°, sometimes considerably more, and it gives way to open turf of the Thero-Airion type only on locally-parched soils over the fractured tops of rock exposures in drier foothills and on warmer, south-facing slopes. The two communities overlap a little in their national distributions and the floristic and environmental contrasts between them in this zone are well seen in sample sets from south-west Scotland (Birse 1980), Shropshire (Sinker *et al.* 1985) and Durham (Hughes & Huntley 1986).

To the opposite climatic extreme, the *Festuca-Agrostis-Galium* grassland is limited by very cold and wet conditions, the influence of which is seen throughout the range of the community in its general exclusion from the higher slopes of the montane zone, and regionally in its scarcity at increasingly lower altitudes in moving into the far north-west of Britain. There, through most of the western Highlands, where rainfall exceeds 1600 mm yr^{-1} (*Climatological Atlas* 1952) with more than 200 wet days yr^{-1} (Ratcliffe 1968) and where the mean annual maximum temperature is usually below 22 °C (Conolly & Dahl 1970), the *Festuca-Agrostis-Galium* grassland is generally reduced to widely-scattered and small stands (McVean & Ratcliffe 1962, King & Nicholson 1964). And elsewhere through the uplands, wherever such inhospitable conditions are approached over higher ground, they help set a general upper limit for the community. Floristically, such effects are reflected in the infrequency here of more strictly montane plants: the Arctic-Subarctic *Deschampsia cespitosa* ssp. *alpina* and Arctic-Alpine *Carex bigelowii* occur occasionally, but their low cover and the scarcity of other species such as *Alchemilla alpina* and *Polytrichum alpinum* help distinguish the *Festuca-Agrostis-Galium* grassland from such more montane vegetation types as the *Deschampsia-Galium* grassland and grassier forms of *Carex-Racomitrium* heath.

As a general rule, the upper altitudinal limit of the *Festuca-Agrostis-Galium* grassland rises with the shift to increasingly drier and warmer regions of the uplands, though some of this effect is lost because of the scarcity of higher mountains in the south of the country, and it is also much affected by physiography and treatments. Overall, the community is only rarely found at heights above 800 m and, across much of its range, is strongly concentrated between 150 and 500 m. At these levels, it is widespread through most of our upland areas, particularly in the Grampians and Southern Uplands, the Lake District and parts of the Pennines, through Wales and the Marches and down into the moors of the south-west of England. In extreme cases, stands can be found virtually down to sea-level, though many tracts of suitable soils at low altitudes have been improved for agriculture and it is mainly along unenclosed stretches of sea-cliffs, out of reach of salt-spray, that the *Festuca-Agrostis-Galium* grassland attains its lowest limits. In such situations, along the western seaboard of Britain and through the Isles, the community can acquire a more oceanic character with species such as *Blechnum spicant*, *Carex binervis* and *Scilla verna* increasing in frequency somewhat. But true maritime influence is uncommon, though plants like *Plantago coronopus*, *P. maritima* and *Armeria maritima* are occasionally found in cliff-top stands and additional sampling in this habitat might permit the recognition of a further distinctive sub-community in which such species were a more consistent feature.

Between these various climatic extremes, the *Festuca-Agrostis-Galium* grassland is found on a range of acidic soils weathered from a diversity of more pervious parent materials. Lime-poor substrates predominate, with the community occurring widely over many different arenaceous and some argillaceous sedimentaries and igneous and metamorphic rocks that make up the bulk of the landscape of upland Britain, and on the lighter and more coarse-textured of the superficials widespread within the limits of glaciation. It is replaced by other more calcicolous vegetation where eluviation is offset by flushing with calcareous waters and is noticeably scarce over tracts of drift-free limestones, like those of Carboniferous age in the Yorkshire and Derbyshire dales, and on the more calcareous of the Dalradian metasediments in the Grampians, though in very rainy climates even profiles derived from lime-rich materials can become sufficiently surface-leached to support this kind of grassland. In such transitional situations and around base-rich flushes, it can become harder to characterise this vegetation but, in general, calcicolous plants are poorly represented. The more catholic *Thymus praecox* and *Carex panicea* find an occasional place in the sward, but species such as *C. pulicaris*, *Briza media*, *Linum catharticum*, *Selaginella selaginoides*, *Ctenidium molluscum* and *Tortella tortuosa*, which help distinguish the *Festuca-*

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Agrostis-Thymus grassland, the basiphile counterpart to this community through the sub-montane zone, are typically very scarce. To the opposite edaphic extreme, the *Festuca-Agrostis-Galium* grassland seems to avoid the most acidic and impoverished substrates like quartzites, and the surface pH is not usually extremely low, being most commonly between 4 and 5.5. Floristically, this is reflected in the somewhat muted calcifuge character of many of the swards included here, with plants like *Luzula campestris*, *Danthonia decumbens*, *Ranunculus acris*, *Viola riviniana* and *Carex pilulifera* quite well represented throughout.

Differences among the soil types, which range from rankers, through brown earths and brown podzolic profiles, to podzols proper, with sometimes a modest amount of gleying in the profile, reinforce the direct influence of climate on the vegetation and produce other effects on their own which help to differentiate the various kinds of *Festuca-Agrostis-Galium* grassland. The Typical sub-community can be seen as the central type in both edaphic and climatic terms. It is the most widespread form, occurring extensively at modest altitudes, mostly between 200 and 400 m, throughout the uplands in areas where rainfall is moderate to heavy, with 800–1200 mm and 140–180 wet days yr^{-1} (*Climatological Atlas* 1952, Ratcliffe 1968), and the summers fairly cool, mean annual maxima being 24–26 °C (Conolly & Dahl 1970). It can be found, over steeper slopes and around rock exposures, on rankers, but it is most characteristic of more mature profiles, usually brown earths and brown podzolic soils, thoroughly leached of any cations and of low base-status, but not very strongly podzolised. The soils are often quite well structured, at least above, and frequently have moder humus rather than mor; and, though kept moist for much of the year, they are generally permeable, with free to moderate drainage or at most only slight seasonal impedence (King 1962, King & Nicholson 1964, Birse 1980). Even where flushed, as is sometimes the case on alluvial flats, or over the lower slopes of hillsides which gather rainwater run-off from above or which experience modest irrigation from seepage lines, there is relatively unhindered through-put. Such flushing helps prevent any hint of stagnation in the profile and offsets the effects of extreme eluviation, both factors which can help maintain the Typical sub-community in areas of higher rainfall: river terraces and irrigated slopes provide very characteristic local habitats for this vegetation in the north-west Highlands and on Skye, for example (McVean & Ratcliffe 1962, Birks 1973). But always in such situations, the waters are characteristically poor in lime and nutrients: the Typical sub-community encompasses a range of more or less calcifuge swards but in general preserves the overall floristic features of the *Festuca-Agrostis-Galium* grassland without any representation of stricter calcicoles and only an occasional mesophytic element. Elsewhere in the uplands this is a very abundant element in rough grazings, providing the mainstay of pastoral agriculture on unenclosed slopes, where it is particularly associated with profiles like those of the very widespread Denbigh and Manod associations (Bradley 1976, *Soil Survey* 1983, Rudeforth *et al.* 1984). The soils are rarely improved by fertilising, usually receiving no manure apart from the dung of the stock, though the extent of this kind of grassland has often been increased by draining more gentle hill slopes carrying poorer-quality swards.

With the shift on to higher ground outside the very wet and cold western Highlands, Typical *Festuca-Agrostis-Galium* grassland tends to be replaced by the swards of the *Vaccinium-Deschampsia* sub-community. This kind of vegetation is most common between 300 and 500 m, though it can extend to lower altitudes on cooler, sunless aspects and, on steeper ground through the Southern Uplands, the Lake District and Wales, can take the community to its upper limit of around 800 m. Annual precipitation is generally over 1200 mm with more than 180 wet days yr^{-1} (*Climatological Atlas* 1952, Ratcliffe 1968) and the mean annual maximum temperature is often less than 24 °C, particularly to the north (Conolly & Dahl 1970). Under such conditions, leaching is often very marked with negligible amounts of exchangeable calcium and a superficial pH that is usually less than 4.5 and frequently as low as 3.5. Sometimes, the soils are quite deep and mature, showing a well-developed podzolic profile but, particularly on steeper ground, where this kind of grassland is often seen, they are shallow and more rock-dominated, sometimes having a strong orange colour below that betokens iron mobilisation and deposition (McVean & Ratcliffe 1962), but frequently amounting to little more than thin accumulations of organic material and mineral detritus. Also distinctive is the fact that the humus here is usually of the mor type, often forming a distinct top that is but slowly integrated into the profile. In moister situations, as on higher slopes of shaded aspect, this can be kept in an almost greasy condition, and on gentler ground, particularly where there are smears of less permeable drift beneath, this kind of *Festuca-Agrostis-Galium* grassland can extend a little way on to stagnohumic gleys which form intergrades to true peats. Generally, though, drainage is free, indeed sometimes excessive, such that on sunny, rocky slopes, there can even be a slight tendency to parching in dry periods of summer weather. Floristically, these edaphic features are reflected in the *Vaccinium-Deschampsia* sub-community in a more thoroughly calcifuge composition with *Galium saxatile* and, more strikingly, *Vaccinium myrtillus*, *Deschampsia flexuosa* and *Pleurozium schreberi* preferentially frequent, and the mesophytic element of the

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community, represented by species such as *Viola riviniana*, *Holcus lanatus*, *Achillea millefolium*, *Cerastium fontanum* and *Plantago lanceolata*, at a minimum, often scarcely visible at all. Such swards are clearly transitional in composition and physiognomy to grassy subshrub vegetation like that of the *Vaccinium-Deschampsia* heath and treatments very likely play an important part in mediating switches from the one to the other (see below). The kinds of stock pastured and the intensity of grazing are also involved in the spread into this type of *Festuca-Agrostis-Galium* grassland of *Nardus stricta*, although this grass also tends to favour the moister humic soils of an impoverished character that are best represented here.

On damper soils of a less base-poor and impoverished character, and particularly through the colder and wetter parts of the uplands, where the *Festuca-Agrostis-Galium* grassland begins to reach one of its climatic limits, the community is usually represented by fairly local and small stands of the *Luzula-Rhytidiadelphus* type. Although found at scattered localities through the Grampians and Southern Uplands, with far-flung sites in northern England and Wales, this is by and large a vegetation type of the western Highlands where the climatic conditions are such as to keep many generally suitable soils in too moist a state for the vigour of the Typical sub-community and to encourage a mildly montane element in the flora. The profiles derived from more lime-poor parent materials can be of the stagnopodzolic type, where a measure of drainage impedence results from the formation of a thin iron pan, while in other cases impervious drift below induces some gleying in the profile; but many of the soils seem to be free-draining, with precipitation or irrigation being the main cause of their permanently moist condition, perhaps with some effect from snow-melt on higher ground, and the profiles being of a flushed brown earth or brown podzolic type. Again, there is often some surface accumulation of organic matter, though this is sometimes of the moder type rather than mor, and the surface pH in these soils can be over 5.5, with measurable amounts of exchangeable calcium (McVean & Ratcliffe 1962, King 1962, King & Nicholson 1964). The damp and often quite humic conditions are reflected here in the replacement of *Luzula campestris* by *L. multiflora* and the preferential frequency of *Agrostis canina* ssp. *canina*, *Viola palustris*, *Carex panicea*, *C. echinata*, *Rhytidiadelphus loreus* and *Thuidium tamariscinum*. *Luzula sylvatica* can get a hold on the fresher soils, though it is often grazed hard back, and more diagnostic of the edaphic conditions usual beneath this sub-community is *Deschampsia cespitosa*. At lower altitudes, this is ssp. *cespitosa*, when the swards included here look very much like a sub-montane replacement for the *Deschampsia-Holcus* grassland of lowland mesotrophic gleys: some of the *Festuca-Agrostis* vegetation with *D. cespitosa* described by King (1962, King & Nicholson 1964) is of this type. In the western Highlands, however, it is ssp. *alpina* that is the more usual taxon, when the *Luzula-Rhytidiadelphus* sub-community can be seen as transitional to the *Deschampsia-Galium* grassland. This is a distinctly montane vegetation type and often mildly chionophilous, so the gradation is to some extent a climatic one, but at intermediate altitudes treatments may mediate the change from what is a largely anthropogenic grassland to one which is not (McVean & Ratcliffe 1962).

Although some of the *Luzula-Rhytidiadelphus* swards can have a fairly mesophytic character, it is in the *Holcus-Trifolium* sub-community that this aspect of the flora reaches its best development. This kind of *Festuca-Agrostis-Galium* grassland is typical of lower altitudes, generally between 100 and 250 m, where the climate is warmer and drier than through much of the range. Annual precipitation is usually around 1000 mm, somewhat more around the fringes of the Southern Uplands, considerably less through the Welsh Marches, with generally not more than 160 wet days yr^{-1} (*Climatological Atlas* 1952, Ratcliffe 1968) and with mean annual maximum temperatures often above 26 °C (Conolly & Dahl 1970). More particularly, the growing season can start up to a couple of weeks earlier and last a month or so longer than over the higher ground where the Typical sub-community is the usual form of *Festuca-Agrostis-Galium* grassland (Smith 1976). Furthermore, the soils here are among the most fertile of those supporting this community, being generally of the brown earth type, well structured and often with mull humus. There is sometimes evidence of surface leaching, especially in lighter-textured profiles in rainier parts of the range, but surface pH is frequently above 5.5. Precipitation and, on occasion, slight flushing help keep the soils free of any tendency to parching, even where they are better-drained and on steeper slopes, and there is quite often a tendency to gleying below where argillaceous bedrocks or clayey drift have provided the parent materials. In some cases, the less oligotrophic and base-poor character of the profiles is attributable to their derivation from substrates which are not themselves extremely poor in composition: through southern Scotland, parts of the Lake District and much of western Wales, for example, the *Holcus-Trifolium* sub-community often occurs on soils weathered from Silurian shales, while in the Marches Triassic rocks and Old Red Sandstone are important parent materials; in the south-west, too, Devonian rocks occur beneath many stands with extensive tracts also on Carboniferous shales and Culm Measures; then, there are many areas where clayey superficials have made a substantial contribution. And, in extreme cases, the local occurrence of such parent materials can support the *Holcus-Trifolium* sub-

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community in unusually harsh climatic conditions (Hughes 1958).

Very commonly, though, the soils here have also been improved somewhat by the addition of lime to offset the tendency to leaching and by compounds like basic slag and, more recently, ratio fertilisers to raise productivity. For this kind of *Festuca-Agrostis-Galium* grassland often occurs in enclosed pastures around the upland fringes, where modest improvement of land taken in at the limits of enclosure has aimed to increase the amount and quality of grazing above that available over the open slopes. More strictly calcifuge plants, such as *Galium saxatile*, *Vaccinium myrtillus*, *Deschampsia flexuosa*, *Pleurozium schreberi* and *Hylocomium splendens* thus tend to have a lesser role here than in other sub-communities, while the mesotrophic conditions are reflected by such good mull indicators as *Holcus lanatus*, *Trifolium repens*, *Achillea millefolium*, *Cerastium fontanum*, *Prunella vulgaris*, *Plantago lanceolata* and *Cynosurus cristatus*. *Lolium perenne* has sometimes been topsown into these swards, particularly through the south-west and up the Marches, but its relative scarcity is one good separation from more calcifuge grasslands of the *Lolio-Cynosuretum*. These can also be found through the upland margins, but they have generally been derived by ploughing and re-seeding and they require a more sustained level of improvement to keep them in good heart (Figure 32). The *Holcus-Trifolium* swards are not so productive as the *Lolio-Cynosuretum*, retaining relatively little green herbage through the winter months, but they are of considerable importance through the dairying areas of western Britain, such as Devon and Cornwall, the hills of Shropshire and the fringes of the Berwyn and Clwyd hills (Page 1980). They are also widely used throughout the range for the winter pasturing of sheep brought down from the open hill land and the concentration of natural manuring provided by these stock is of considerable importance in maintaining the soil fertility. Smaller stands of the *Holcus-Trifolium* sub-community also extend along verges of roads and tracks through the upland margins and mark out places where, over the unenclosed slopes, sheep lie up: such areas can develop a luxuriance of growth very striking against the surrounding close-cropped swards.

The remaining kind of *Festuca-Agrostis-Galium* grassland, the *Lathyrus-Stachys* sub-community, shows some floristic similarities to the *Holcus-Trifolium* type, particularly where this has developed from light-textured drift that is showing some marginal effects of surface leaching, but it is related to rather more particular edaphic conditions. It is best known from the accounts of vegetation in the Derbyshire Dales (Balme 1954, Grime 1963*a*,*b*, Pigott 1970*a*) where it forms an integral part of a sequence of communities deployed over the dale sides and tops. This zonation is described below but, in the present context, what is important is that the *Lathyrus-Stachys* sub-community represents an occurrence of *Festuca-Agrostis-Galium* grassland over a calcareous substrate, in this case Carboniferous Limestone, towards the climatic limits of the range of the community. The controlling influence of the very lime-rich bedrock has to be strongly masked for this kind of vegetation to develop in areas such as Derbyshire where the annual rainfall is only about 1000 mm (Clapham 1969) and, in this particular case, it is distinctive mixtures of long-weathered limestone products augmented by substantial amounts of loess that comprise the bulk of the drift (Pigott 1962). Most of the plateau soils developed from this mantle have been enclosed and variously improved but, in places, more strongly leached profiles have good stands of the *Vaccinium-Deschampsia* sub-community on well-defined podzols (Balme 1953, Grime 1963*b*, Pigott 1970*a*). Where the mask of superficials thins, however, as it does over the brow tops of the dales, with some downwash of material on to the steep limestone slopes below, the *Lathyrus-Stachys* sub-community can be found over brown earths with some surface eluviation and a superficial pH of 4.5 to 5, but with a continuing mild influence from more calcareous material below. Here, then, there is the distinctive lingering presence of calcicoles such as *Avenula pratensis*, *Sanguisorba minor* and *Helianthemum nummularium*, the occasional records for early calcifuge invaders like *Deschampsia flexuosa*, *Galium saxatile* and *Vaccinium myrtillus*, the background of mesophytes such as *Achillea millefolium*, *Galium verum*, *Lotus corniculatus* and *Campanula rotundifolia*, and the very striking group of preferentials, *Lathyrus montanus*, *Stachys betonica*, *Succisa pratensis* and *Carex caryophyllea*, together in this part of Britain with *Viola lutea* (Balme 1954). Similar vegetation to the *Lathyrus-Stachys* sub-community has been seen under comparable edaphic and climatic conditions on the Mendips, though samples have not been included here.

Over this considerable variety of soil types across its range, the *Festuca-Agrostis-Galium* grassland is always a plagioclimax community dependent ultimately for its maintenance on grazing by stock, with some influence too from deer, rabbits and hares (e.g. King & Nicholson 1964). It has been derived originally, by clearance, burning and grazing, from what was probably quite a variety of more calcifuge woodland types, perhaps with some contribution from sub-shrub vegetation towards higher altitudes, such that today it occurs very widely through the forest zone, with some extension above into the low-alpine, comprising most of the better-quality rough grazings beyond, and sometimes just within, the limits of enclosure. The history of these swards is long and complex, probably beginning in many areas with the sporadic clearances of the Neolithic, but it seems

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Figure 32. Floristic transition from calcifugous to mesotrophic grassland with agricultural improvement on more free-draining brown soils around the upland fringes.

	U4a		U4b		MG6b	
Agrostis capillaris	V	(1–10)	V	(1–8)	V	(4–8)
Anthoxanthum odoratum	V	(1–10)	V	(1–8)	V	(1–7)
Festuca rubra	III	(1–8)	IV	(1–8)	IV	(2–8)
Festuca ovina	V	(1–19)	III	(1–8)	I	(2–4)
Potentilla erecta	V	(1–6)	III	(1–4)	I	(1–3)
Galium saxatile	IV	(1–6)	III	(1–4)		
Pleurozium schreberi	III	(1–6)	I	(1–2)		
Deschampsia flexuosa	II	(1–6)	I	(1–6)		
Nardus stricta	II	(1–6)	I	(1–4)		
Vaccinium myrtillus	II	(1–6)				
Holcus lanatus	II	(1–6)	V	(1–6)	V	(2–6)
Achillea millefolium	III	(1–6)	IV	(1–6)	II	(2–5)
Trifolium repens	II	(1–6)	IV	(1–6)	V	(1–8)
Cerastium fontanum	II	(1–4)	IV	(1–4)	V	(1–5)
Poa pratensis	II	(1–6)	III	(1–7)	III	(1–5)
Cynosurus cristatus	I	(1–3)	II	(1–3)	V	(2–7)
Lolium perenne			II	(1–5)	V	(2–7)
Ranunculus acris	I	(1–4)	II	(1–4)	IV	(1–5)
Dactylis glomerata	I	(1–3)	II	(1–4)	III	(1–4)
Taraxacum officinale agg.	I	(1–3)	II	(1–4)	II	(1–3)
Bellis perennis			II	(1–6)	II	(1–4)
Trifolium pratense			II	(2–5)	II	(1–7)
Cirsium arvense	I	(1–3)	I	(1–4)	II	(1–5)
Cirsium arvense	I	(1–3)	I	(1–4)	II	(1–5)
Leontodon autumnalis					II	(1–4)
Poa trivialis					II	(2–5)
Bromus hordeaceus hordeaceus					II	(1–6)
Rhytidiadelphus squarrosus	IV	(1–10)	III	(1–8)	II	(1–6)
Luzula campestris	IV	(1–4)	III	(1–3)	II	(1–5)
Plantago lanceolata	II	(1–4)	III	(1–4)	III	(1–5)
Rumex acetosa	II	(1–4)	III	(1–4)	III	(1–4)
Number of samples	172		35		43	
Number of species/sample	22	(7–62)	20	(11–39)	14	(4–26)

U4a *Festuca–Agrostis–Galium* grassland, Typical sub-community
U4b *Festuca–Agrostis–Galium* grassland, *Holcus–Trifolium* sub-community
MG6b *Lolio–Cynosuretum, Anthoxanthum* sub-community

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certain that, in the more accessible parts of the uplands, as through the south-west, in much of Wales, the Lake District and the Southern Uplands, substantial areas of some kind of pasture were established as early as the medieval period, with an extension over the next few centuries to remoter regions like the Highlands (Roberts 1959, Steven & Carlisle 1959, King & Nicholson 1964, Pearsall & Pennington 1973, Harvey & St Leger-Gordon 1974).

The exact character of these grasslands, the more immediate forebears of our present rough grazings, can only be guessed at, but it is evident from the records that they were often treated in a different fashion from today and this may be safely assumed to have affected their composition. Frequently, in these earlier days, the upland grazings were used as summer pasture in a system of transhumance and, among the stock, cattle were at least as important as sheep, sometimes more so (Franklin 1952, Roberts 1959). From the mid-1700s, with the introduction of improved sheep breeds, the balance among the grazing animals began to shift in the other direction, often substantially so, and, with the coincidental spread of enclosure of the lower slopes, the foundations of the modern kinds of sheep-rearing that prevail today through most of the uplands were established. Often, now, the sheep are left on the unenclosed grazings for much of the year, as in the 'heaf' or 'heft' system that has been the basis of pastoralism through the Southern Uplands and Pennines for more than two centuries, with the flocks largely self-sustaining in home ranges on the hills, and with some wintering of vulnerable stock, like first-year ewe lambs, on the enclosed pasture below (Trow-Smith 1957, King & Nicholson 1964, Pearsall & Pennington 1973).

Of the different kinds of grasslands, heaths and mires that make up the varied patchworks of rough grazing through the uplands, the *Festuca-Agrostis-Galium* swards are among the vegetation most favoured by sheep. In those parts of the country where the community is proportionately important, as in the Southern Uplands, considerably higher stocking densities can be sustained on the open hills: there, Hunter (1961) recorded values of one ewe per 0.6 ha, as opposed to one ewe per more than 4 ha in those regions where poorer-quality vegetation predominated. At its best in this area, it can experience grazing intensities twice those felt by rushy vegetation like the *Juncus-Galium* pasture and three times those on grassy *Molinia-Potentilla* mire (Hunter 1954, 1962, see also Boulet 1939). Compared with these communities, the *Festuca-Agrostis-Galium* grassland presents generally palatable mixtures of plants, and its composition and physiognomy now reflect the sustained impact of the close and choosy cropping characteristically associated with sheep, particularly with the breeding ewes which have largely replaced the less selective wethers popular in the days when mutton, rather than young lamb, was favoured for the table (Roberts 1959, Spedding 1971, Grant *et al.* 1985). And, where the vegetation types occur in mosaics, there seems to be marked seasonality in the way in which present-day flocks graze these different elements, with the *Festuca-Agrostis-Galium* grassland being cropped more in summer than in winter, the less palatable swards turned to more often as herbage becomes scarce (Hunter 1954, 1962).

The overall effect of this kind of predation is to keep the vegetation short and varied, with the distinctive mixed dominance of a number of more or less fine-leaved grasses, together with grazing-resistant hemicryptophytes, and to set back repeatedly any spread of sub-shrubs or invasion by shrubs and trees. Behind such a general influence, however, there is undoubtedly a great diversity of subtle and shifting interactions between sward and stock which give every stand of this really rather well defined vegetation its own peculiarities of history and structure. For one thing, there is within the community itself considerable variety in the grazing value of the herbage that is dependent partly on edaphic differences. The best quality swards fall mostly within the *Holcus-Trifolium* sub-community, some of which are good enough to qualify as 'third-grade rye-grass pastures' and, whether more productive because of lying on naturally more mesotrophic soils or by virtue of improvement by manuring and top-sowing, these are often of great importance in supplementing the available grazing over generally poor tracts of pasture on the open hills (e.g. Hughes 1958) or during the lean months of winter where stock are brought down on to enclosed stands. Close behind among the more widely distributed kinds of *Festuca-Agrostis-Galium* grassland are the swards of the Typical sub-community and probably, also, some of the *Vaccinium-Deschampsia* type, where these provide some relief among mosaics of heath, a common occurrence (Hunter 1962). To the opposite extreme, lies the coarser herbage in the *Vaccinium-Deschampsia* sub-community, which can extend on to soils highly favourable for the expansion of *Nardus*: such swards can experience grazing intensities less than half those on the better quality grassland (Hunter 1962).

And probably very important, too, for the way in which the kinds of vegetation included here are preferred, one against the other, by the grazing stock, and selected over other components of rough grazings, are the proportions and patterns in which all the various grasslands, heaths and mires are disposed before the flocks on a particular stretch of the uplands. This means that the floristic and physiognomic definition of the more favoured elements, like the different types of *Festuca-Agrostis-Galium* grassland, is partly dependent upon the character of the whole mosaic of vegetation

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types and the ways in which this is exploited by the stock. Of particular importance, in this respect, is the vulnerability of these swards to the spread of species such as *Nardus* and *Pteridium*, the checks on which may be balanced quite delicately (see below).

Zonation and succession

Through the open grazings of the sub-montane west and north of Britain, the *Festuca-Agrostis-Galium* grassland can be found with a great variety of other grasslands, heaths and mires, in diverse patchworks that reflect differences in regional climate across its wide range, and variations in soils and treatments over particular stretches of hills. Grazing is of prime importance in preventing the regression of the community to woody vegetation and, though it is possible that towards its very highest limits some stands would revert to climax heath, most would be succeeded by scrub and woodland if treatment ceased. In altitudinal sequences, then, this is a community of the forest zone and sub-alpine transition, limited above by the harsh climate and now curtailed below by enclosure and improvement.

The *Festuca-Agrostis-Galium* grassland makes its maximum contribution to upland rough grazings on the well-drained, acidic soils characteristic of steeper slopes underlain by lime-poor substrates, and some of the commonest zonations in which it is seen are related to shifts from these favoured geological, topographic and edaphic conditions, particularly as they affect the moisture regime, base-status and trophic state of the soils. For example, the community often extends on to shallow rankers, provided these are not disposed among boulders or on ledges inaccessible to grazing stock, where shrubs and trees can invade, but where there is any tendency for such soils to become parched in dry weather, the *Festuca-Agrostis-Galium* grassland is usually replaced by more fragmentary swards of the Thero-Airion type. Such transitions are best seen over small, fractured rock outcrops around the drier southern and eastern fringes of the uplands (Jarvis 1974, Sinker *et al.* 1985, Hughes & Huntley 1986), though they persist locally in wetter regions on warmer, south-facing slopes (Birse 1980), and they often involve a switch to the *Festuca-Agrostis-Rumex* grassland. In such situations, the thinning and increased droughtiness of the soil cover is marked by a change to a more open and tussocky turf, lacking such species as *Anthoxanthum*, *Potentilla erecta*, *Luzula campestris* and *Viola riviniana*, together with the bulky pleurocarpous mosses, but gaining plants like *Rumex acetosella*, *Aira praecox*, *Poa annua* and other ephemerals, *Sedum anglicum* and acrocarpous mosses.

Much more extensive and important, though, are those patterns related to increased moisture of the soil, which can be a function of higher precipitation and run-off, flushing or drainage impedence. Sometimes the changes are fairly subtle, relating to a slight lessening of slope and accumulation of downwashed colluvial material, when the deeper and better integrated profiles can be marked just by a shift from Typical *Festuca-Agrostis-Galium* grassland to the more mesophytic *Holcus-Trifolium* sub-community. A similar change, sometimes amounting to little more than a rise in the frequency of *H. lanatus*, *T. repens*, *Achillea millefolium* and *Cerastium fontanum*, can accompany the move from arenaceous parent materials to more argillaceous ones, quite a slight increase of clay in the profile being sufficient to slow down leaching, raise the base-status a little and improve the texture. Such patterns can be seen where the sandstones are replaced by shales in sequences of Devonian, Silurian and Carboniferous rocks such as underlie much of south-west England, Wales and the Southern Uplands, the change in geology often being matched by a shift from steeper and craggier slopes to more gentle ground. Or, where slopes lessen, there can be smears of clayey drift which mask the controlling influence of pervious sandstones. In all these cases, the move from shedding towards receiving drainage helps confirm the lithological influence of the parent materials.

Very commonly, however, the impedence of run-off in situations like this is such as to effect a more marked floristic change. Characteristically, over the lower ground through the uplands, high rainfall and water shed from surrounding hills induces surface-water gleying over impermeable substrates on gentle slopes, brown earths or podzolised profiles being replaced by stagnogleys or where, in impeded hollows, there is some shallow fluctuation of the water-table, by ground-water gleys. Then, the *Festuca-Agrostis-Galium* grassland typically gives way to the *Juncus-Galium* mire, physiognomically a rush-pasture, dominated by clumps of *J. acutiflorus* or *J. effusus*, and with such Molinietalia associates as *Galium palustre*, *Cirsium palustre*, *Lotus uliginosus*, *Ranunculus flammula* and *Angelica sylvestris*. Sometimes, where the underlying edaphic differences are sharp, the floristic junctions are correspondingly abrupt, but where it is drift that is the primary control on drainage, then the changes are much more gradual. Boundaries can be further blurred where, as is usually the case, stock have access, when an ill-defined mosaic of vegetation types is produced among the clumps of unpalatable rushes. Receiving most of the attention of the grazing stock, the swards between get a concentration of dung and then a Cynosurion element can become prominent in the transition, with the *Holcus-Trifolium* sub-community surrounding the clumps of rush-pasture and giving way on steeper slopes to Typical *Festuca-Agrostis-Galium* grassland. There can be a marked drift of more mesophytic plants in such situa-

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tions, with species like *Festuca rubra*, *H. lanatus* and *T. repens* well represented throughout. Very often, too, patchworks of this kind have been further improved by draining of the wetter ground, with the consequent expansion of the *Festuca-Agrostis-Galium* grassland, the application of artificials like basic slag helping to maintain higher fertility and favouring the *Holcus-Trifolium* sub-community. Much pasture upgraded in this way has been taken in towards the limits of enclosure and sometimes given more assiduous improvement, but neglect can allow quite rapid reversion to a rush-pasture mosaic where the drains become blocked, and the toing and froing of land around the fringes of the uplands between these vegetation types is often a reflection of the state of the agricultural economy. Mixtures of the communities figure prominently in the pastures described from the Cheviots by King (1962; see also King & Nicholson 1964) and very extensive tracts occur over the undulating foothills of central Wales and the Southern Uplands.

Gleyed mineral soils of the kinds which support these transitions from the *Festuca-Agrostis-Galium* grassland to the *Juncus-Galium* rush-pasture can readily accumulate a humose topsoil in the wetter parts of the country and the resultant humic gleys and stagnohumic gleys are often intergrades to acid peats proper which have built up over benches and plateaus and in waterlogged hollows through western and northern Britain. In some such situations, the zonations described above form just part of extensive vegetation sequences which run on into Ericion wet heath and Erico-Sphagnion blanket mire on thickening ombrogenous peat that has developed over increasingly gentle slopes, running back from scarps to shelving dips, up from steep slopes on to high-altitude plateaus or down to low-level benches. In other cases, the *Juncus-Galium* rush-pasture forms a transition zone on the gleyed surrounds to water-tracks and flushes running through *Festuca-Agrostis-Galium* grassland, a common feature where steeper hill slopes channel run-off into juvenile streams or where impermeable rocks or drift bring soil waters to the surface within stretches of open pasture. Then, the *Juncus-Galium* vegetation usually gives way in turn to a strip of rush-dominated *Carex echinata-Sphagnum* mire over the irrigated peaty soil but grazing and trampling can fret the boundaries of these zonations and maintain patches of grassy sward among clumps of rushes in close juxtaposition with the *Sphagnum* carpet of the flushed ground.

A frequent complication of these kinds of soil-related patterns where the *Festuca-Agrostis-Galium* grassland occurs among better-aerated peaty profiles at lower altitudes in the western part of its range is the spread of *Molinia*. In contrast to the *Juncus-Galium* rush-pasture, the *Molinia-Potentilla* mire, which contains most of the *Molinia*-dominated swards in this part of the country, is characteristically associated with areas of quickening drainage through peaty mineral soils and true peats, and it can often be seen among stretches of *Festuca-Agrostis-Galium* grassland towards the western seaboard of Britain, around the heads and sides of moorland streams and fringing soligenous and basin mires (McVean & Ratcliffe 1962, Ratcliffe & Hattey 1982). In such edaphic and climatic conditions, *Molina* can be very vigorous, its dominance marking out the boundary between one vegetation type and the other quite clearly, but where the *Molinia-Potentilla* mire has been burned and grazed, a common practice, continuing predation by stock can maintain fairly short and diverse swards over the peatier soils, and the floristic continuity is then considerable. The *Anthoxanthum* sub-community of the *Molinia-Potentilla* mire, for example, has frequent *Anthoxanthum*, *Agrostis capillaris*, *Festuca rubra*, *Holcus lanatus* and *Potentilla erecta*, and occurs very extensively with *Festuca-Agrostis-Galium* grassland in Wales and south-west Scotland. Similar vegetation can also be found over shallow ombrogenous peats where wet heath has been transformed into grassy *Molinia* mire by burning and grazing.

In the cool and wet conditions at higher altitudes, the spread of *Nardus* presents a different complication to the picture. This grass is of varying frequency through the *Festuca-Agrostis-Galium* grassland and its abundance is always strongly influenced by the treatments which the swards have received. But edaphically, it competes least well on the well-drained moder and mull soils characteristic of the Typical and *Holcus-Trifolium* sub-communities, rather better on some of the cold humic gleys that, in the western Highlands, can carry the *Luzula-Rhytidiadelphus* sub-community, and best of all on profiles which combine a humose topsoil with a strongly-leached and oligotrophic mineral base, often gleyed (e.g. Pearsall 1968). In some of the transitions already mentioned, *Nardus* can increase its cover where there is a tendency for such soils to develop, so that a zone of *Nardus-Galium* grassland becomes interposed in the sequences: this can happen over much-trampled transitions between the *Festuca-Agrostis-Galium* grassland and *Carex echinata-Sphagnum* mire towards higher altitudes, where the community gives way to ill-drained stretches of *Molinia-Potentilla* mire, and where, over redistributed peat washed down from above, there is a zonation to run-down wet heath and blanket mire (e.g. Smith 1918). Very frequently, too, *Nardus* spreads within the *Vaccinium-Deschampsia* sub-community where it extends on to humic stagnopodzols, a common feature on drift-smeared slopes at higher altitudes, and then there can be a patchy mosaic of *Festuca-Agrostis-Galium* and *Nardus-Galium* grasslands. In such situations, the latter community is often readily picked out in winter by the abundant bleached herbage of the mat-

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grass but the two vegetation types have many associates in common: *Festuca ovina*, *Agrostis capillaris*, *Deschampsia flexuosa*, *Potentilla erecta*, *Galium saxatile*, *Vaccinium myrtillus* and pleurocarpous mosses all provide strong continuity through the swards. It has been suggested (Heddle & Ogg 1936, Fenton 1937, Harris 1939) that the spread of *Nardus* into the *Festuca-Agrostis-Galium* grassland in situations such as these is a consequence of the historical switch from cattle to sheep as the major grazing stock and, more recently, from wethers to the more selective breeding ewes (Roberts 1959, Grant *et al.* 1985). Where *Nardus* is becoming entrenched, it may thus now require densities of sheep to control it which are unacceptably high for the continued health of the better-quality *Festuca-Agrostis-Galium* grassland (Nicholson *et al.* 1970), such that the mat-grass continues its advance or becomes firmly entrenched in sharply-defined mosaics.

In all of the zonations described so far, there is generally a marked poverty of bases in all the soils, but different kinds of pattern can be seen where this situation is relieved, either by some change in parent materials or by irrigation of the profiles by lime-rich waters. Through most of its range, the *Festuca-Agrostis-Galium* grassland is replaced in such circumstances by the *Festuca-Agrostis-Thymus* grassland, a community with which it shares many catholic and mildly calcifuge herbs, but where there is fairly consistent enrichment with plants such as *Thymus praecox*, *Carex panicea*, *C. pulicaris*, *Selaginella selaginoides* and calcicolous bryophytes. The two vegetation types come closest over drier soils, as where there is a change from brown earths of low base-status to those with a higher pH and calcium content where, say, limy partings occur among base-deficient shales or a drift cover thins over native calcareous rocks: then, the *Festuca-Agrostis-Thymus* grassland is usually represented by the *Trifolium-Luzula* sub-community which can grade almost imperceptibly into Typical *Festuca-Agrostis-Galium* grassland or the *Holcus-Trifolium* sub-community. More striking patterns are to be seen around base-rich flushes where, within the space of a few metres, there can be a transition from Typical *Festuca-Agrostis-Galium* grassland over the unirrigated sopes, through the *Carex* sub-community of the *Festuca-Agrostis-Thymus* grassland to a Caricion davallianae mire on a calcareous gley, with perhaps a Cratoneurion spring at its head. At moderate altitudes through the northern part of the range of the *Festuca-Agrostis-Galium* grassland, the small-sedge mire vegetation in such zonations is usually of the *Pinguiculo-Caricetum* type, with the *Carici-Saxifragetum* replacing it in stony flushes over higher ground. At higher altitudes, too, over moderately base-rich mulls through the Scottish Highlands, the *Festuca-Agrostis-Alchemilla* grass-heath can figure in such sequences. *Alchemilla alpina* and *T. praecox* are good indicators of transitions to this kind of vegetation with, in moister situations, basiphilous small sedges but, again, there can be considerable floristic continuity through the swards.

With the move southwards into the Craven district, it is the *Sesleria-Galium* grassland that constitutes the more calcicolous element in grassland patchworks of this type, marking out extensive stretches of calcareous lithomorphic soils, with the *Festuca-Agrostis-Galium* grassland limited to places where surface leaching of native profiles is more pronounced or where the influence of the underlying bedrock is masked by light-textured drift. A comparable situation pertains in the Derbyshire Dales, towards the south-eastern limit of the *Festuca-Agrostis-Galium* grassland, although here the climate is sufficiently warm and dry for the *Festuca-Avenula* grassland to occupy the rendzina soils on the steeper valley sides, with the distinctive *Lathyrus-Stachys* sub-community of the more calcifuge grassland marking out the loess-contaminated soils on the brow tops (Balme 1953, Pigott 1962, Grime 1963*a*,*b*). More natural sequences here can run on into the *Vaccinium-Deschampsia* sub-community with *D. flexuosa* showing a tendency to invade and acidify the shallower and less base-poor soils and consequently modifying the floristics and structure of the *Lathyrus-Stachys* sub-community (Grime 1963*b*, Pigott 1970*a*) but, in many places, the deeper soils of the plateau have been improved so that, beyond a field boundary, there is often a sharp change to the *Holcus-Trifolium* sub-community or a Cynosurion sward.

In all these patterns, grazing is usually the major factor in preventing the reversion of the *Festuca-Agrostis-Galium* grassland and the other plagioclimax swards with which it occurs to the different kinds of forest from which they were, in the main, originally derived. The effects of a reduction in grazing pressure are widely seen among tracts of the community where the ground becomes naturally less accessible to the stock, as where there are tumbles of blocky talus over the slopes, or where crags and ravines interrupt the landscape, although in such places the change in topography often affects soil development and climate, so that the transitions to lush herbaceous or woody vegetation seen there are usually of complex origin. More obviously seral are those situations where stock have been temporarily or permanently withdrawn from the open pastures, reflecting the fate of local farming enterprises or the vicissitudes of the agricultural economy as a whole, with a neglect of the grazings or enclosure for alternative purposes such as forestry or water resource management. In fact, the continuing high value of the better-quality elements among our rough pastures, like the *Festuca-Agrostis-Galium* grassland, means that such opportunities for succession are fairly scarce. Where

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they do occur, the first invaders are often birch, usually *Betula pubescens* but with *B. pendula* locally prominent in some places, as through parts of east-central Scotland, and *Sorbus aucuparia*, with pines frequently seeding in from plantations, and oaks, generally *Quercus petraea* but locally *Q. robur*, sometimes coming in later (Pearsall & Pennington 1973). On the more base-poor and rocky soils supporting the *Festuca-Agrostis-Galium* grassland, such species would probably eventually come to dominate in the kind of vegetation we see in the *Quercus-Betula-Dicranum* woodland, the field layer of which can present virtually identical mixtures of plants to those found here in the *Vaccinium-Deschampsia* sub-community and some of the more unremittingly calcifuge Typical stands. Over less impoverished soils on to which the grassland extends, where *Corylus avellana* or even *Crataegus monogyna* can sometimes be found among the early colonisers after withdrawal of grazing, the seral trend is probably towards the *Quercus-Betula-Oxalis* woodland, a forest type whose herbaceous element is akin to the more mesophytic *Festuca-Agrostis-Galium* swards, such as are included in the Typical, *Holcus-Trifolium* and *Luzula-Rhytidiadelphus* sub-communities. Both these woodland communities are widespread through the northern and western sub-montane zone of Britain and can often be seen in close association with the *Festuca-Agrostis-Galium* grassland, though not commonly in active successional development from it. More commonly, the woodlands occur as an enclosed element in the landscape towards the lower altitudinal limits of the grassland or extend up through it in fragmentary fashion in inaccessible ravines. Or, they are open to the stock, offering valuable sheltered grazing in hard weather and often being in the later stages of conversion back to pasture after a period of enclosure for coppicing, rarely practised now: such woodlands, with their characteristically grassy field layers, are often essentially *Festuca-Agrostis-Galium* swards with a canopy of over-mature trees.

Even where there are reductions in grazing of *Festuca-Agrostis-Galium* grassland, however, the progression to woodland is by no means assured. In the first place, seed-parents of some important potential invaders, like the oaks, are very scarce through much of the sub-montane zone. Others, like the birches and pines, whose seed is numerous and widely dispersed by the wind, need an open well-lit turf for establishment, and suitable conditions can be very short-lived before the development of a rank tussocky sward precludes further establishment. Then, there is the possibility of expansion of sub-shrubs previously held in check but readily able to form a heathy cover in which trees can get a hold only with difficulty. *Calluna* and *V. myrtillus* can both be found with varying degrees of frequency as sparse sprigs in the sward and can become important dominants in heaths developed from *Festuca-Agrostis-Galium* grassland with, less commonly, *Ulex minor*, *U. gallii*, *Erica cinerea* and *Empetrum nigrum* ssp. *nigrum* playing a part in various parts of the range. Through the sub-montane zone, the community is found very commonly in mosaics with various kinds of heath, the balance between burning and grazing playing a controlling role in determining their proportions as plagioclimax replacements for forest and the direction of successional shifts between them. The *Calluna-Ulex minor* heath in the New Forest and around Poole Harbour towards the south-eastern climatic limit of the *Festuca-Agrostis-Galium* grassland, the *Calluna-Ulex gallii* heath at lower altitudes through the south-west of England and Wales, the *Calluna-Erica cinerea* heath in the western parts of Scotland, the *Calluna-Scilla* heath around the maritime fringe, the *Calluna-Vaccinium* heath in the less oceanic parts of the sub-montane zone and the *Calluna-Deschampsia* heath through the polluted southern Pennines – all these can occur in patchworks with or gradations to the *Festuca-Agrostis-Galium* grassland and some of them have distinct sub-communities representing spatial or seral transitions to it. Towards its highest altitudinal limits, the community can also be found with the *Vaccinium-Deschampsia* heath and it is possible that, just beyond the forest zone, this is an original precursor to high-level stands. Another shrub which commonly features in *Festuca-Agrostis-Galium* grassland towards lower altitudes is *Ulex europaeus* and transitions to patches of *Ulex-Rubus* scrub often mark out the sites of old settlements or disturbed boundary banks in tracts of the pasture, pathways through it or enclosures which have passed in and out of intensive use for grazing.

The other highly significant development which can supervene in the regression of neglected *Festuca-Agrostis-Galium* grassland is the spread of *Pteridium aquilinum*. Typically, through the sub-montane zone, this fern grows most vigorously on colluvial soils, over which it is abundant in the two kinds of woodland from which the *Festuca-Agrostis-Galium* grassland has commonly developed. Many of the slope-foot stands of dense *Pteridium-Galium* vegetation to be seen today throughout the unenclosed rough grazings of the uplands no doubt derive directly from the field layers of cleared forest, but bracken has increased its extent very considerably through what were once open pastures. Changes in treatment are certainly partly to blame for this: bracken is no longer cut as it once was for bedding, and the shift towards grazing almost exclusively with sheep means that the advancing fronts of fronds no longer get the heavy trampling that cattle used to give them. Transitions between the *Festuca-Agrostis-Galium* grassland and the *Pteridium-Galium* vegetation can be very gradual, and species such as *Potentilla erecta*, *Galium*

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saxatile and *Dicranum scoparium* can run on sparsely under quite dense covers of fronds, but much pasture with bracken is virtually useless once the annual cover of shoots is well grown and the re-establishment of trees where grazing is abandoned completely is well nigh impossible.

Distribution

The *Festuca-Agrostis-Galium* grassland is virtually ubiquitous through much of the sub-montane zone, although it becomes patchy in the Grampians and distinctly scarce through the western Highlands. The most widespread form is the Typical sub-community, with the *Holcus-Trifolium* sub-community very common towards lower altitudes, the *Vaccinium-Deschampsia* type extending on to higher slopes through most of the range, with the *Luzula-Rhytidiadelphus* sub-community on higher ground to the north. The *Lathyrus-Stachys* sub-community occurs very locally in the Derbyshire Dales and probably elsewhere.

Affinities

This community subsumes the bulk of what has become popularly known in Britain as '*Festuca-Agrostis* grassland', although the application of this term has been diverse and often imprecise. In fact, in the earliest accounts (summarised in Tansley 1911), the more fine-leaved swards included in what was then termed 'siliceous grassland' received little attention compared with vegetation dominated by *Nardus* or *Molinia*, and it was only with the agriculturalists' concern to recognise different grades of hill pasture (e.g. Stapledon 1937), that a more precise floristic account of the better-quality grasslands was attempted (Tansley 1939). The similarity of the upland fringe grassland to grazed calcifuge swards and 'grass-heath' familiar from lowland Britain was immediately apparent, but although the resemblance and contrasts have been pointed out in a number of studies (Watt 1940, Sinker *et al.* 1985, Hughes & Huntley 1986), they have not so far been satisfactorily resolved within a national framework. In this scheme, the more open and often ephemeral-rich turf of drought-prone acid soils in the south and east is placed in the *Festuca-Agrostis-Rumex* grassland, which intergrades with the *Festuca-Agrostis-Galium* grassland through the upland fringes but which has very obvious affinities with the Thero-Airion alliance. To the other side of this major climatic and edaphic divide, the calcifuge swards included here are clearly of the Nardo-Galion type, with preferential records for species such as *Luzula campestris*, *Carex pilulifera*, *Potentilla erecta* and *Danthonia decumbens*.

Even in some earlier accounts, the existence of different kinds of *Festuca-Agrostis* grassland in the northern and western sub-montane zone was hinted at, and occasionally demonstrated in detailed local studies, like Balme's (1953) account of zones within her *Festuceto-Agrostidetum* in Derbyshire. But it was not until McVean & Ratcliffe's (1962) separation of 'species-poor' and 'species-rich' types among their *Agrosto-Festucetum* in the Scottish Highlands that the foundation was laid for a more comprehensive understanding of variation among these grasslands. In one form or another, their distinction between more calcifuge and more calcicole swards has been found to be a generally applicable and useful one (e.g. Ward *et al.* 1972*a*, Birks 1973, Evans *et al.* 1977, Ferreira 1978) and it persists in this scheme in the recognition of a *Festuca-Agrostis-Thymus* grassland as the more basiphile and generally richer counterpart to the *Festuca-Agrostis-Galium* grassland. The two communities grade into one another extensively, particularly on drier mesotrophic soils, a feature which led Birse (1980, 1984) to recombine elements of them in a single *Achilleo-Festucetum*. But, although both can be accommodated in the Nardo-Galion, the *Festuca-Agrostis-Thymus* grassland can usually be clearly distinguished as a transition to Caricion davallianae small-sedge mire vegetation often having such species as *Selaginella selaginoides*, *Carex panicea*, *C. pulicaris* and calcicolous bryophtes along with *Thymus praecox*. As with McVean & Ratcliffe (1962), this scheme also recognises a *Festuca-Agrostis-Alchemilla* grass-heath, in some ways floristically intermediate between the two other grasslands, but also with a more montane character.

Another important strand of variation among these vegetation types is less visible among the data of McVean & Ratcliffe (1962) than in studies concentrating on grasslands at lower altitudes and latitudes, as in the account of the '*Festuca-Agrostis* complex' of the Cheviots by King (1962; see also King & Nicholson 1964) and the description of pastures through the Southern Uplands by Hill & Evans (1978). In the schemes of these workers, there are more mesophytic kinds of *Festuca-Agrostis* grassland, sometimes improved a little for grazing, which correspond essentially with less productive swards among lowland neutral grasslands of western Britain like the *Anthoxantho-Festucetum* of Page (1980). Here, the gradation is to Cynosurion vegetation of much improved and re-seeded agricultural grassland with species like *Cynosurus cristatus*, *Trifolium repens*, *Holcus lanatus* and *Achillea millefolium* providing a strong floristic link. But it is sensible to retain such transitional swards within the *Festuca-Agrostis-Galium* grassland, and here they are characterised as the *Holcus-Trifolium* sub-community, the Typical form of the grassland corresponding more closely to what those following McVean & Ratcliffe (1962) understood as mainstream *Festuca-Agrostis* grassland.

Both McVean & Ratcliffe (1962) and King & Nichol-

https://doi.org/10.1017/9780521391665.039 Published online by Cambridge University Press

son (1964) also acknowledged the difficulty of separating their *Festuca-Agrostis* communities from other calcifuge grasslands of the uplands, particularly those in which *Nardus* played an important role. In this scheme, a separate *Nardus-Galium* grassland is recognised, though it shows an extensive overlap in its climatic and edaphic preferences with the *Festuca-Agrostis-Galium* grassland and shares many associates, separation between the communities sometimes being a matter of the cover of *Nardus*. This is a crude and pragmatic solution but a sensible one which recognises that, while *Nardus* can have a strong hold here, notably in the *Vaccinium-Deschampsia* sub-community, its expansion depends on the fulfilment of particular habitat requirements, not least a distinct style of treatment. The relationships to the *Juncus-Festuca* vegetation, where *J. squarrosus* is the dominant, can pose similar difficulties, though this is nothing like as common a problem. And, though some of the *Luzula-Rhytidiadelphus* swards represent a link with the *Deschampsia-Galium* grassland, the separation from this more montane and chionophilous community, essentially a replacement for the *Festuca-Agrostis-Galium* grassland through the western Highlands, is generally clear.

The other important floristic affinities of the community are with a variety of kinds of sub-shrub vegetation. For the most part, gradations to these are under the control of anthropogenic factors, with burning and grazing maintaining zonations and successions from grassland to heath. Again, transitions can be gradual and complex, with all manner of intermediates and mosaics widely represented in all parts of the country, and the only way of coping with more difficult situations is by resorting to dominance of the one element or the other. In phytosociological terms, the close relationship of these different kinds of vegetation is reflected in their inclusion together in separate orders, the Nardetalia and Calluno-Ulicetalia within the same class, the Nardo-Callunetea.

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Floristic table U4

	a	b
Agrostis capillaris	V (1–10)	V (1–8)
Anthoxanthum odoratum	V (1–8)	V (1–6)
Potentilla erecta	V (1–6)	III (1–4)
Festuca ovina	V (1–10)	III (1–8)
Galium saxatile	IV (1–6)	III (1–4)
Holcus lanatus	II (1–6)	V (1–6)
Achillea millefolium	III (1–6)	IV (1–6)
Trifolium repens	II (1–6)	IV (1–6)
Cerastium fontanum	II (1–4)	IV (1–4)
Poa pratensis	II (1–6)	III (1–7)
Prunella vulgaris	I (1–4)	II (1–4)
Cynosurus cristatus	I (1–3)	II (1–3)
Dactylis glomerata	I (1–3)	II (1–4)
Veronica chamaedrys	I (1–6)	II (1–4)
Taraxacum officinale agg.	I (1–3)	II (1–4)
Bellis perennis		II (1–6)
Lolium perenne		II (1–5)
Trifolium pratense		II (2–5)
Alopecurus pratensis		I (1–4)
Campanula rotundifolia	II (1–4)	I (1–4)
Galium verum	I (1–4)	II (1–3)
Lathyrus montanus	I (1–4)	I (1–3)
Lotus corniculatus	II (1–4)	II (1–4)
Succisa pratensis	I (1–6)	II (1–3)
Stachys betonica		
Avenula pratensis		
Viola lutea	I (1–4)	
Carex caryophyllea	I (1–4)	
Anemone nemorosa		
Briza media		I (3)
Sanguisorba minor		

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c	d	e	4
V (4–7)	IV (1–8)	V (1–8)	V (1–10)
V (2–7)	V (1–6)	III (1–6)	V (1–8)
V (2–4)	V (1–6)	V (1–6)	V (1–6)
V (4–8)	IV (1–10)	IV (1–10)	IV (1–10)
III (2–7)	V (1–4)	V (1–8)	IV (1–8)
II (1–4)	II (1–6)	I (1–3)	II (1–6)
III (2)	I (1–3)		II (1–6)
II (2)	I (1–4)		II (1–6)
	II (1–3)		II (1–4)
I (2)	I (1–3)		II (1–7)
	I (1–3)		I (1–4)
I (2)	I (1–3)	I (1–3)	I (1–3)
I (1–3)			I (1–4)
I (2)			I (1–6)
I (1–4)			I (1–4)
I (1–4)			I (1–6)
			I (1–5)
			I (2–5)
			I (1–4)
IV (2)	I (1–3)	I (1–3)	I (1–4)
IV (2–4)			II (1–4)
IV (2–4)	I (1)		I (1–4)
III (1–4)	I (1–6)		II (1–6)
III (2–5)	II (1–4)		I (1–6)
III (2–6)			I (2–6)
III (2–4)		I (1–2)	I (1–4)
II (2–4)		I (1–4)	I (1–4)
II (2–4)		I (1–3)	I (1–4)
II (1–7)		I (1–3)	I (1–7)
II (2)			I (2–3)
II (1–4)			I (1–4)

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Floristic table U4 (*cont.*)

	a	b	c	d	e	4
Luzula multiflora	I (1–4)	I (1–3)	I (4)	IV (1–6)	I (1–4)	II (1–6)
Rhytidiadelphus loreus	I (1–4)	I (1–3)		III (1–8)	I (1–3)	I (1–8)
Deschampsia cespitosa	I (1–4)	I (1–4)	II (2–5)	III (1–10)	I (1–4)	I (1–10)
Thuidium tamariscinum	I (1–4)	I (1–3)		III (1–8)		I (1–8)
Agrostis canina canina	I (1–4)	I (1–3)		III (1–8)		I (1–8)
Carex panicea	I (1–4)	I (1–4)	I (1–2)	II (1–4)	I (1–3)	I (1–4)
Viola palustris	I (1–6)	I (1–3)		II (1–4)	I (1–6)	I (1–6)
Luzula sylvatica	I (1–6)			II (1–4)	I (1–2)	I (1–6)
Blechnum spicant	I (1–6)			II (1–4)	I (1–3)	I (1–6)
Carex echinata	I (1–3)			II (1–3)	I (1–3)	I (1–3)
Vaccinium myrtillus	II (1–6)		II (1–4)	I (1–4)	V (1–6)	II (1–6)
Pleurozium schreberi	III (1–6)	I (1–2)	II (2)	II (1–6)	IV (1–6)	II (1–6)
Nardus stricta	II (1–6)	I (1–4)	I (2–4)	III (1–6)	IV (1–8)	II (1–8)
Deschampsia flexuosa	II (1–6)	I (1–6)	I (4–6)	II (1–6)	IV (1–9)	II (1–9)
Pteridium aquilinum	I (1–6)	I (1–4)	I (8)	I (1–4)	II (1–4)	I (1–8)
Racomitrium lanuginosum	I (1–3)			I (1–4)	II (1–4)	I (1–4)
Rhytidiadelphus squarrosus	IV (1–10)	III (1–8)	II (1–2)	IV (1–6)	III (1–6)	III (1–10)
Luzula campestris	IV (1–4)	III (1–3)	IV (2–5)	II (1–3)	III (1–4)	III (1–5)
Festuca rubra	III (1–8)	IV (1–8)	II (1–4)	III (1–6)	II (1–8)	III (1–8)
Hypnum cupressiforme s.l.	III (1–6)	II (1–3)	II (1–2)	II (1–4)	III (1–4)	III (1–6)
Dicranum scoparium	III (1–6)	I (1–3)	II (2)	I (1–3)	III (1–6)	III (1–6)
Viola riviniana	III (1–4)	II (1–4)	III (1–2)	III (1–4)	I (1–3)	III (1–4)
Pseudoscleropodium purum	III (1–6)	II (1–6)	I (2–4)	II (1–4)	II (1–4)	II (1–6)
Hylocomium splendens	III (1–10)	I (1–6)	I (2)	III (1–6)	II (1–6)	II (1–10)
Plantago lanceolata	II (1–4)	III (1–4)	III (1–2)	I (1–3)		II (1–4)
Rumex acetosa	II (1–4)	III (1–4)	III (1–2)	II (1–4)		II (1–4)
Danthonia decumbens	II (1–6)	I (1–6)	II (2–5)	I (1–4)	II (1–6)	II (1–6)
Ranunculus acris	I (1–4)	II (1–4)	II (1–2)	II (1–4)	I (1–3)	II (1–4)
Carex pilulifera	III (1–6)	I (1–3)	I (2)	II (1–4)	I (1–2)	II (1–6)
Calluna vulgaris	II (1–4)	I (1–3)	I (2–4)	I (1–4)	II (1–6)	II (1–6)
Veronica officinalis	II (1–4)	I (1–2)	II (1–2)	I (1–4)		I (1–4)
Juncus squarrosus	I (1–4)	I (1–3)		II (1–4)	II (1–4)	I (1–4)

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Polytrichum commune	I (1–6)	I (1–3)
Carex binervis	I (1–6)	
Polygala serpyllifolia	I (1–3)	I (1–3)
Agrostis canina montana	I (1–6)	I (1–3)
Conopodium majus	I (1–6)	I (1–4)
Mnium hornum	I (1–4)	I (1–3)
Euphrasia officinalis	I (1–4)	I (1–4)
Molinia caerulea	I (1–4)	I (1–4)
Oxalis acetosella	I (1–3)	
Thymus praecox	I (1–6)	I (1–5)
Juncus effusus	I (1–4)	I (1–4)
Holcus mollis	I (1–8)	I (1–6)
Polytrichum alpinum	I (1–4)	I (1–6)
Rhytidiadelphus triquetrus	I (1–6)	I (1–3)
Lophocolea bidentata s.l.	I (1–3)	I (1–3)
Cirsium vulgare	I (1–4)	I (1–3)
Cirsium arvense	I (1–3)	I (1–4)
Carex nigra	I (1–4)	I (1–3)
Ranunculus repens	I (1–4)	I (1–4)
Poa annua	I (1–4)	I (1–3)
Number of samples	172	35
Number of species/sample	22 (7–62)	20 (11–39)
Herb height (cm)	13 (2–66)	13 (2–50)
Herb cover (%)	96 (70–100)	94 (60–100)
Ground layer height (mm)	20 (10–70)	15 (10–20)
Ground layer cover (%)	20 (0–95)	15 (0–80)
Altitude (m)	294 (2–853)	181 (2–457)
Slope (°)	13 (0–90)	14 (0–80)

a Typical sub-community
b *Holcus lanatus-Trifolium repens* sub-community
c *Lathyrus montanus-Stachys betonica* sub-community
d *Luzula multiflora-Rhytidiadelphus loreus* sub-community
e *Vaccinium myrtillus-Deschampsia flexuosa* sub-community
4 *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland (total)

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	II (1–4)	II (1–6)	I (1–6)
	II (1–3)	II (1–4)	I (1–6)
I (2–4)	I (1–3)	I (1–3)	I (1–4)
I (4–5)	I (1–3)	I (1–4)	I (1–6)
I (1–4)	I (1–3)	I (1–3)	I (1–6)
I (1–4)	I (1–3)		I (1–4)
	I (1–3)	I (1–3)	I (1–4)
	I (1–6)	I (1–3)	I (1–6)
	I (1–3)	I (1–4)	I (1–4)
I (1)	I (1–4)	I (1–3)	I (1–6)
	I (1–3)	I (1–3)	I (1–4)
	I (1–8)	I (1–3)	I (1–8)
	I (1–4)		I (1–6)
	I (1–4)		I (1–6)
	I (1–3)		I (1–3)
	I (1–3)		I (1–4)
	I (1–3)		I (1–4)
	I (1–3)		I (1–4)
	I (1–3)		I (1–4)
	I (1–3)		I (1–4)
18	51	66	342
28 (18–42)	24 (13–34)	17 (8–30)	22 (7–62)
no data	17 (6–42)	11 (2–42)	13 (2–66)
no data	93 (25–100)	88 (10–100)	94 (25–100)
no data	29 (10–60)	24 (10–50)	22 (10–70)
no data	28 (0–80)	11 (0–95)	17 (0–95)
no data	430 (50–1021)	400 (150–760)	319 (2–1021)
22 (0–35)	15 (0–55)	21 (0–90)	17 (0–90)

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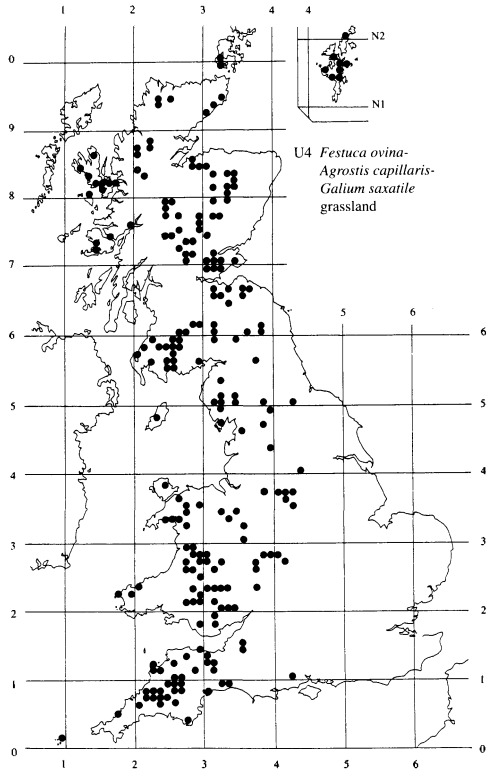

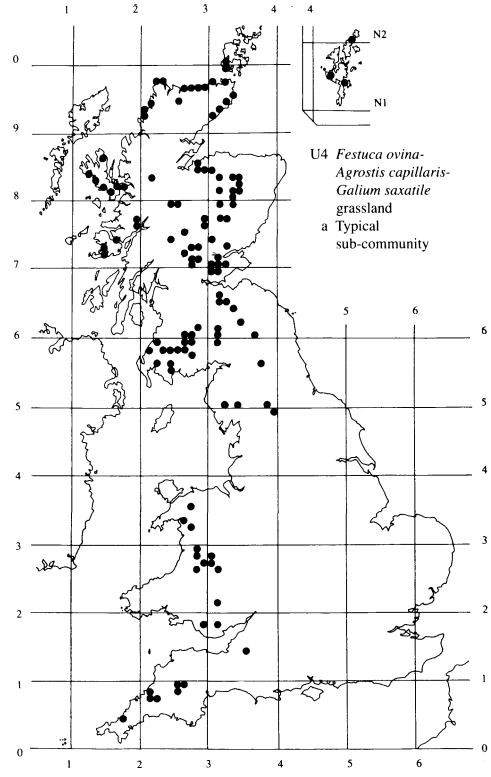

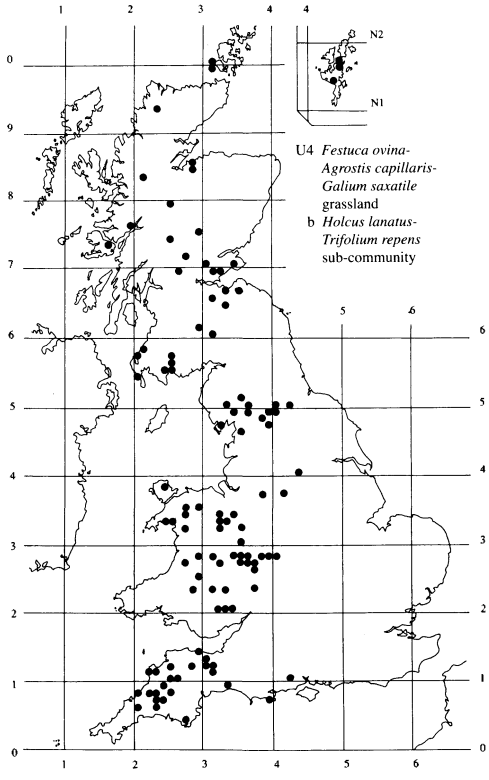

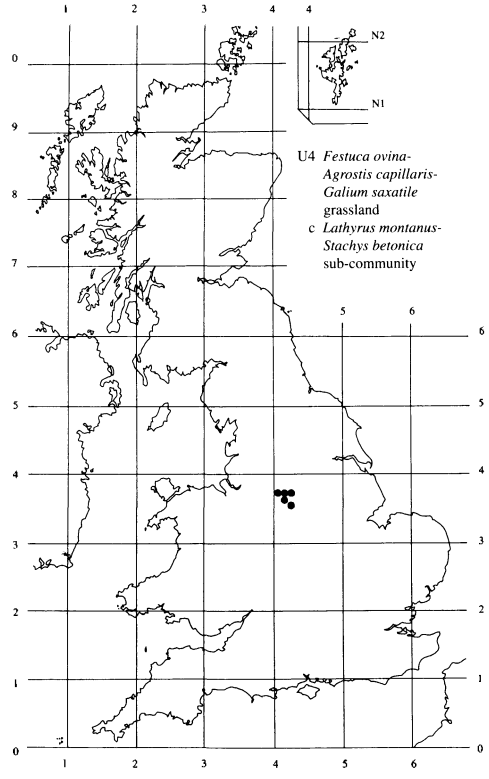

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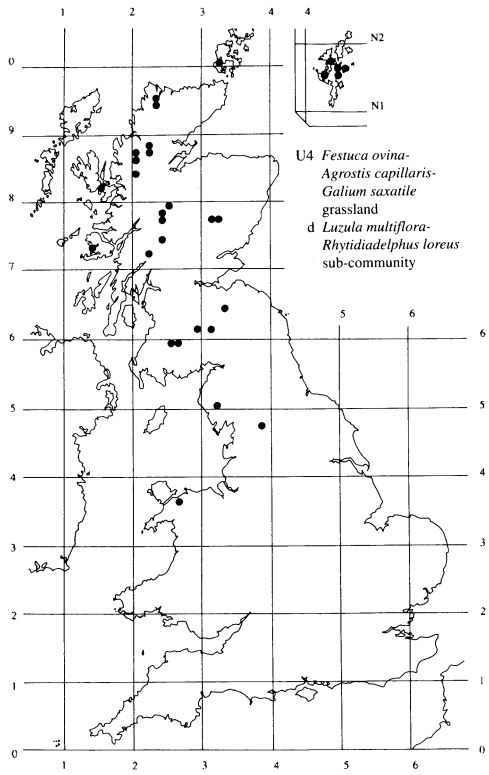

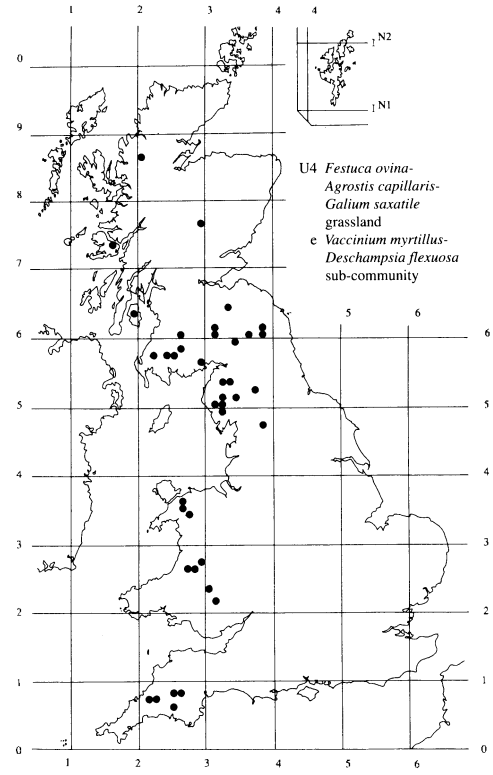

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