
M10

Carex dioica-*Pinguicula vulgaris* mire

Pinguiculo-Caricetum dioicae Jones 1973 *emend.*

Synonymy

Carex hostiana-*C. demissa* nodum Poore 1955b; *Carex demissa*-*C. panicea* nodum Poore 1955b *p.p.*; Flush vegetation Holdgate 1955a *p.p.*; Turfy marshes Pigott 1956a; Gravel flushes Pigott 1956a; Calcareous marsh Sinker 1960; *Carex panicea*-*Campyllum stellatum* nodum McVean & Ratcliffe 1962; *Schoenus nigricans* provisional nodum McVean & Ratcliffe 1962 *p.p.*; *Kobresieto-Caricetum* Ratcliffe 1965 *p.p.*; *Gymnostometo-Caricetum* Ratcliffe 1965; *Caricetum lepidocarpae-hostianae* Shimwell 1968a; *Carex panicea*-*Campyllum stellatum* Association Birks 1973; *Eriophorum latifolium*-*Carex hostiana* Association Birks 1973; *Schoenus nigricans* Association Birks 1973 *p.p.*; *Pinguiculo-Caricetum dioicae* Jones 1973 *p.p.*; *Carex fens* Proctor 1974 *p.p.*; *Pinguiculo-Caricetum dioicae* Jones 1973 *emend.* Wheeler 1975; *Schoenus nigricans* Community Birse & Robertson 1976; *Caricetum hostiano-pulicaris* (Birse & Robertson 1976) Birse 1980; *Carici dioicae-Eleocharitetum quinqueflorae* (Birse & Robertson 1976) Birse 1980 *p.p.*; *Anagallis tenella-Equisetum variegatum* Association Birse 1980; *Campylio-Caricetum dioicae* Dierssen 1982; *Eleocharitetum quinqueflorae* Dierssen 1982; *Schoenus ferrugineus* stands Wheeler *et al.* 1983 *p.p.*

Constant species

Carex dioica, *C. hostiana*, *C. lepidocarpa*, *C. panicea*, *C. pulicaris*, *Eriophorum angustifolium*, *Juncus articulatus*, *Pinguicula vulgaris*, *Aneura pinguis*, *Bryum pseudotriquetrum*, *Campyllum stellatum*, *Ctenidium molluscum*, *Drepanocladus revolvens*.

Rare species

Bartsia alpina, *Carex capillaris*, *Equisetum variegatum*, *Juncus alpinus*, *Kobresia simpliciuscula*, *Minuartia stricta*, *M. verna*, *Primula farinosa*, *Schoenus ferrugineus*, *Sesleria albicans*.

Physiognomy

The *Pinguiculo-Caricetum dioicae* includes some of the most distinctive of our more calcicolous flush vegetation in which small sedges, dicotyledons and bryophytes predominate, usually forming the bulk of a short sward, often hummocky and open. Although there is a strong contingent of constant species, the community is very variable in its composition, showing some marked differences in the proportions of its more frequent species and in the representation of groups of plants preferential to particular habitats or regions. And, where certain of these species are abundant, they can have a striking effect on the physiognomy of the vegetation. The habitat conditions, too, can have a marked influence on the appearance of the community. Most stands are grazed and the herbage is accordingly often cropped very short; where herbivore pressure is not so high, the vegetation can have a more luxuriant look, hemicryptophyte dicotyledons especially making an obvious contribution. Then, various factors contribute to the openness of the sward and there is often some deposition of tufa beneath the herbage which can produce a hummocky structure and give the turf a very characteristic crunchy texture. Frequently, then, there is a fine mosaic of micro-topographies within the vegetation which allows species of wetter and drier ground, and of more stable and disturbed areas, to grow closely juxtaposed.

The *Pinguiculo-Caricetum* is essentially a small-sedge mire and, among the more frequent Carices, *C. panicea*, *C. dioica*, *C. lepidocarpa*, *C. hostiana*, *C. pulicaris* can all occur in abundance, either together or in vegetation more obviously dominated by one or another species. *C. nigra* is also frequent in many stands and *C. demissa* and *C. echinata* or *C. flacca* are common in some sub-communities or their variants. Despite the very considerable variation among these commoner sedges, this particular combination of species is shared only by the closely-related *Carici-Saxifragetum aizoidis* and, even

there, there are some obvious differences in the balance of those represented. Bulkier sedges, such as *tend* to predominate in swamper base-rich mires, are rarely present, though *C. rostrata* sometimes occurs. Finally, among this element, the community provides one locus for the rare *C. capillaris*.

Other cyperaceous plants can also be prominent. *Eriophorum angustifolium* is very frequent throughout and *Eleocharis quinqueflora* is common, especially in Scottish stands, and can be abundant. *Schoenus nigricans* also occurs here in some very distinctive flushes and so does the recently-rediscovered *S. ferrugineus*. *Kobresia simpliciuscula* can be a local dominant and *Eriophorum latifolium* occurs in some variants. *Scirpus cespitosus* is typically rare, though it can be well represented in transitional surrounds to the community where it occurs within blanket mire or wet heath.

Among other monocotyledons, certain rushes and grasses occur frequently. *Juncus articulatus* is a constant of the community, *J. bulbosus/kochii* is very typical of less markedly base-rich sites and, in some variants, *J. alpinus* and *J. triglumis* occur. *J. acutiflorus* and *J. squarrosus* occur very sparsely. *Molinia caerulea* is the commonest grass overall and locally it can dominate. *Festuca ovina* is rather more variable in its occurrence but, with species such as *Briza media*, *Sesleria albicans* and *Agrostis stolonifera*, it is very characteristic of the *Briza-Primula* sub-community which typically occurs within the context of Mesobromion grasslands. Other grasses found more occasionally include *Anthoxanthum odoratum*, *Festuca rubra* and *Nardus stricta*, all of which tend to increase where the community interrupts stretches of more calcifugous swards. *Triglochin palustris* and *Tofieldia pusilla* are typical of some variants of the community and *Narthecium ossifragum* of others.

The other herbs of the *Pinguiculo-Caricetum* generally occur as scattered plants and again they can show considerable variety, the frequency of particular species representing transitions in a number of directions. Very frequent throughout and distinctive of this kind of mire are *Pinguicula vulgaris* and *Selaginella selaginoides*, both of them plants which are rare within the Caricion nigrae poor fens. Then, in many stands, there is some *Potentilla erecta* and *Succisa pratensis* and, rather more unevenly represented, *Equisetum palustre*, and *Euphrasia officinalis* agg. Also characteristic, but more obviously preferential to particular sub-communities or their variants are *Linum catharticum*, *Primula farinosa*, *Prunella vulgaris*, *Parnassia palustris*, *Thymus praecox* and *Equisetum variegatum* (in the *Briza-Primula* sub-community) and *Drosera rotundifolia* and *Erica tetralix* (in the *Carex-Juncus* sub-community). Some of these species provide a strong continuity with the vegetation that typically surrounds the flushes of the community and many of them also occur in the closely related *Carici-Saxifrage-*

tum, though *S. aizoides* itself is typically of only local significance here. Apart from *Succisa pratensis*, taller fen herbs are generally uncommon, though in one variant there is a strong enrichment with Molinietales dicotyledons. Among rarer herbs, this community provides a locus for *Bartsia alpina*, *Minuartia verna* and *M. stricta*. Bryophytes are almost always an obvious element in the sward and quite commonly comprise 50% or more of the ground cover, either in extensive carpets among the herbs or as discrete patches or hummocks. More calcicolous species such as *Campyllum stellatum*, *Aneura pinguis*, *Drepanocladus revolvens* (sometimes determined to var. *intermedius*), *Ctenidium molluscum*, *Fissidens adianthoides* and *Cratoneuron commutatum* are among the more frequent species of the community. Also very common is *Bryum pseudotriquetrum* and in particular variants *Scorpidium scorpioides*, *Racomitrium lanuginosum*, *Pellia indiviifolia*, *Ditrichum flexicaule*, *Catascopium nigrum* and *Gymnostomum recurvirostrum*. *Blindia acuta* can also sometimes be found, though it is nothing like so frequent as in the *Carici-Saxifragetum*.

Sub-communities

***Carex demissa-Juncus-bulbosus/kochii* sub-community:** *Carex hostiana-C. demissa* nodum Poore 1955b; *Carex demissa-C. panicea* nodum Poore 1955b p.p.; Flush vegetation Holdgate 1955a p.p.; *Carex panicea-Campyllum stellatum* nodum McVean & Ratcliffe 1962; *Schoenus nigricans* provisional nodum McVean & Ratcliffe 1962 p.p.; *Schoenetum nigricantis* Shimwell 1968a; *Carex panicea-Campyllum stellatum* Association Birks 1973; *Eriophorum latifolium-Carex hostiana* Association Birks 1973; *Schoenus nigricans* Association Birks 1973 p.p.; *Pinguiculo-Caricetum eleocharetosum* Jones 1973 p.p.; *Schoenus nigricans* Community Birse & Robertson 1976; *Caricetum hostiano-pulicaris* (Birse & Robertson 1976) Birse 1980; *Carici dioicae-Eleocharitetum quinqueflorae* (Birse & Robertson 1976) Birse 1980 p.p.; *Schoenus ferrugineus* stands Wheeler *et al.* 1983 p.p. This sub-community comprises the less calcicolous kinds of *Pinguiculo-Caricetum*, a floristic shift that is visible in all the elements of the vegetation. Thus, among the sedges, though *Carex panicea*, *C. dioica*, *C. hostiana* and also *C. nigra* remain very frequent, *C. lepidocarpa* and *C. flacca* are only occasional or sparse, *C. pulicaris* is somewhat patchy and, on the positive side, *C. demissa* and *C. echinata* are preferentially frequent, the former especially being often prominent in the sward. Then, *Juncus bulbosus/kochii* and *Erica tetralix* are considerably more common here than in the other sub-communities and there are occasional records for *Narthecium ossifragum*, *Drosera rotundifolia* and *Scirpus cespitosus* (especially where the community

occurs as flushed areas within ombrogenous mires) or for *Nardus stricta*, *Anthoxanthum odoratum* and *Festuca rubra* (where it interrupts stretches of calcifugous grassland). By contrast, more calcicolous herbs such as *Briza media*, *Primula farinosa*, *Linum catharticum* and *Sesleria albicans* are usually poorly represented. Bryophytes are generally a little less prominent in the sward than in the other sub-communities with species such as *Bryum pseudotriquetrum*, *Fissidens adianthoides* and *Ctenidium molluscum* of rather patchy occurrence, but a varied and locally extensive ground cover can occur and *Campylyum stellatum* and *Scorpidium scorpioides* are often among the most obvious species. Three variants of this sub-community can be recognised, two of rather similar composition, one much more distinctive.

***Eleocharis quinqueflora* variant:** *Carex hostiana*-*C. demissa* nodum Poore 1955b; *Carex demissa*-*C. panicea* nodum Poore 1955b p.p.; *Carex panicea*-*Campylyum stellatum* nodum McVean & Ratcliffe 1962 p.p.; *Carex panicea*-*Campylyum stellatum* Association Birks 1973 p.p.; *Carici dioicae-Eleocharitetum quinqueflorae* Typical subassociation (Birse & Robertson 1976) Birse 1980. In this variant, which is often very wet underfoot and closely associated with spring-heads, *Eleocharis quinqueflora* is preferentially frequent and quite commonly abundant, sharing dominance with the sedges or exceeding them in its cover. And, among the sedges, *C. hostiana* and *C. pulicaris* tend to be rather infrequent. *Erica tetralix*, too, is less common than usual in this sub-community. Associated herbs are relatively few in number (this is the most species-poor kind of *Pinguiculo-Caricetum*) and, though bryophytes can have a quite extensive ground cover, the frequent species are not numerous: apart from *Campylyum stellatum* and *Scorpidium* there is usually just some *Aneura pinguis* and *Drepanocladus revolvens* and occasionally a little *Bryum pseudotriquetrum*.

***Carex hostiana*-*Ctenidium molluscum* variant:** *Carex panicea*-*Campylyum stellatum* nodum McVean & Ratcliffe 1962 p.p.; *Carex panicea*-*Campylyum stellatum* Association Birks 1973 p.p.; *Caricetum hostiano-pulicaris* (Birse & Robertson 1976) Birse 1980. In its general floristics, this variant is very similar to the above, but it does show a noticeable shift in its sedge and bryophyte component. The former generally dominate among the vascular flora, *Eleocharis quinqueflora* being rather infrequent and usually of low cover, but *Carex hostiana* and *C. pulicaris* both show a rise in frequency here and, with *C. panicea*, they are usually the species with the highest cover. Plants of somewhat drier ground are also a little more common, with *Erica tetralix* frequent and locally fairly abundant and *Molinia caerulea*, *Festuca ovina*, *F. rubra* and *Nardus stricta* prominent in the context of flushed grasslands and wet heaths. Among the bryophytes, *Scorpidium* is much less common in this

variant than the former one but *Ctenidium molluscum* becomes common and often contributes a high proportion of the ground cover.

***Schoenus nigricans* variant:** Flush vegetation Holdgate 1955b p.p.; *Schoenus nigricans* provisional nodum McVean & Ratcliffe 1962 p.p.; *Schoenetum nigricantis* Shimwell 1968a; *Eriophorum latifolium*-*Carex hostiana* Association Birks 1973; *Schoenus nigricans* Association Birks 1973; *Pinguiculo-Caricetum dioicae eleocharetosum* Jones 1973 p.p.; *Schoenus nigricans* Community Birse & Robertson 1976; *Schoenus ferrugineus* stands Wheeler *et al.* 1983 p.p. Through the *Pinguiculo-Caricetum* as a whole, *Schoenus nigricans* is only an occasional species but locally it attains high frequency and abundance in this kind of flush vegetation. On balance, this variant clearly belongs in the *Carex-Juncus* sub-community, with common records for such species as *Carex demissa*, *Juncus bulbosus/kochii*, *Erica tetralix* and *Scorpidium scorpioides*, but the prominence of *Schoenus* and the more or less consistent occurrence of some other species make this vegetation very distinct. Thus, *Eriophorum latifolium* is unusually frequent here (it is, generally speaking, a plant of the *Briza-Primula* sub-community) and *Drosera rotundifolia* is commonly accompanied by *D. anglica*, *Pinguicula vulgaris* occasionally by *P. lusitanica*. Then, along with common and sometimes abundant *Molinia*, there can be locally prominent *Myrica gale* and, among the bryophytes, there is frequently some *Blindia acuta*. As well as including many examples of sub-montane *S. nigricans* flushes, this variant also provides a locus for some of the occurrences of the very rare *S. ferrugineus*, recently rediscovered in what is apparently a natural locality in Perthshire (Wheeler *et al.* 1983).

***Briza media-Primula farinosa* sub-community:** Flush vegetation Holdgate 1955a p.p.; Turfy marshes Pigott 1956; Calcareous marsh Sinker 1960; *Kobresieto-Caricetum* Ratcliffe 1965; *Caricetum lepidocarphae-hostianae* Shimwell 1968a; *Pinguiculo-Caricetum eleocharetosum p.p. & equisetosum p.p.* Jones 1973; *Carex fens* Proctor 1974 p.p.; *Pinguiculo-Caricetum dioicae* Jones 1973 emend. Wheeler 1975; *Anagallis tenella-Equisetum variegatum* Association Birse 1980. As in the *Carex-Juncus* sub-community, vascular plants still play a prominent role in the vegetation here, though many of the swards are open with extensive exposures of bare ground and some fine patterning of the different components over the micro-habitats. But in this sub-community calcicoles and more mesophytic herbs are much better represented. Thus, among the community species, *Carex lepidocarpa*, *C. hostiana* and *C. pulicaris* become more consistently frequent and are commonly accompanied by *C. flacca* and, in Upper Teesdale in Durham, by *Kobresia simpliciuscula*. *C. demissa* and *C.*

echinata, by contrast, are scarce. Then, among the preferentials, *Briza media*, *Primula farinosa*, *Linum catharticum*, *Sesleria albicans* and *Equisetum variegatum* occur frequently, *Eriophorum latifolium*, *Juncus alpinus* and *Tofieldia pusilla* rather more occasionally. *Juncus bulbosus/kochii*, *Erica tetralix*, *Narthecium ossifragum* and *Drosera rotundifolia*, on the other hand, are much reduced in their occurrence and only of local significance. Also more common here than in the *Carex-Juncus* sub-community are *Festuca ovina*, *Agrostis stolonifera*, *Thymus praecox*, *Parnassia palustris*, *Prunella vulgaris*, *Euphrasia officinalis* agg. (including *E. confusa* and *E. micrantha* where species have been distinguished), *Leontodon autumnalis* and *Equisetum palustre*. Many of these preferential herbs provide a strong floristic continuity with the Mesobromion swards within which this sub-community typically occurs. The bryophyte element, which is generally prominent, especially in more open stands, also has some distinctive features: among the community species, *Aneura pinguis*, *Ctenidium molluscum* and *Fissidens adianthoides* are more consistently frequent and are often accompanied by *Cratoneuron commutatum*, less commonly by *C. filicinum*, *Calliergon cuspidatum*, *Ditrichum flexicaule* and *Racomitrium lanuginosum*. *Scorpidium scorpioides*, by contrast, is rare.

Three rather distinct variants can be recognised and further sampling may permit the characterisation of a fourth to contain stands which show a general affinity with this sub-community but which lie largely outside the range of such species as *Pinguicula vulgaris*, *Selaginella selaginoides*, *Carex dioica* and *Primula farinosa*. *Anagallis tenella*, generally speaking an uncommon plant in the community, is rather typical of this kind of vegetation which comes close in its floristics to our more base-rich dune slacks (e.g. the *Anagallis* variant of Wheeler's (1975, 1980b) *Pinguiculo-Caricetum* and the *Anagallis-Equisetum* Association of Birse (1980)).

***Cirsium palustre* variant:** *Pinguiculo-Caricetum filipenduletosum* Wheeler 1975. The general features of the sub-community are maintained here, except that species such as *Sesleria albicans*, *Carex dioica* and *Primula farinosa*, whose range is more northern and montane, are of low frequency. More strikingly, the vegetation is consistently enriched by an assemblage of tall herbs most characteristic of Molinieta fen-meadows. *Cirsium palustre*, *Valeriana dioica*, *Filipendula ulmaria*, *Angelica sylvestris* are all very frequent, with *Cardamine pratensis*, *Galium palustre* and *G. uliginosum* and, in wetter stands, *Carex rostrata*, *Menyanthes trifoliata* and *Caltha palustris*. Mixtures of these species, sometimes with much *Molinia*, may predominate over the small-sedge element in this vegetation, creating a quite different appearance from the usual kind of *Pinguiculo-Caricetum* flush; in other stands, *Juncus acutiflorus* is

locally abundant and, very occasionally, *Schoenus nigricans* can dominate. Among the bryophytes, *Calliergon cuspidatum* becomes constant and *Plagiomnium rostratum* and *Cratoneuron filicinum* are frequent.

***Molinia caerulea-Eriophorum latifolium* variant:** Flush vegetation Holdgate 1955a p.p.; Turfy marshes Pigott 1956; Calcareous marsh Sinker 1960; *Caricetum lepidocarpae-hostianae molinietosum* Shimwell 1968a; *Pinguiculo-Caricetum eleocharetosum* p.p. & *equisetosum* p.p. Jones 1973; *Carex fens* Proctor 1974 p.p.; *Pinguiculo-Caricetum molinietosum* Wheeler 1975. This variant preserves the general features of the *Briza-Primula* sub-community much more obviously than the above with rich mixtures of small sedges and short herbaceous associates predominating in a usually close sward. *Carex flacca*, *Briza media*, *Festuca ovina*, *Sesleria caerulea*, *Primula farinosa*, *Linum catharticum*, *Equisetum palustre*, *Triglochin palustris* and *Parnassia palustris* all attain high frequencies along with the community constants. *Molinia* is well represented and it is in this variant that *Eriophorum latifolium* attains its highest frequency in the community. In Upper Teesdale, *Kobresia* is very common and there, too, *Bartsia alpina* and *Carex capillaris* are sometimes found. Among the bryophytes, all the community species are very frequent and, in addition, there is often some *Cratoneuron commutatum* and *Calliergon cuspidatum*.

Where this variant occurs in sites that are gently flushed, diverse mixtures of the above species can form a more or less intact and fairly smooth turf, sometimes dominated by sedges (or, in Upper Teesdale, by *Kobresia*), more rarely by *Molinia*. Grazing usually keeps the sward short but also very frequently the animals puddle the ground into a hummocky structure and wherever any of the factors tending to open up the sward becomes a predominant element in the environment, the vegetation cover (and often its shallow underlying soil) is disrupted, first to form a patchy carpet, then to leave fragments with extensive intervening areas of rock debris. The effects of this process on the floristics and physiognomy of this variant have been well described from Tarn Moor in Cumbria by Holdgate (1955a) and, in more detail, from Upper Teesdale by Pigott (1956a) and Jones (1973; see also Bradshaw & Jones 1976).

What happens in such situations is that, in addition to the fragmentation of the sward, which now appears as perched patches of varying size and shape, new microhabitats are created on the hummock sides, which are often eroded by undercutting with the flushing waters and by wind, and on the intervening very wet bare ground. The hummock sides provide an especially favourable situation for smaller rosette species such as *Pinguicula*, *Primula*, *Parnassia* and *Tofieldia*, as well as for occasional patches of *Saxifraga aizoides*, and also for bryophytes such as *Aneura pinguis*, *Ctenidium molluscum* and

Campylium stellatum: in such places, too, Pigott (1956a) also recorded occasional *Jungermannia atrovirens* and sparse *Leiocolea alpestris* and *Scapania nemorosa* var. *alata*. The gravelly flats in such mosaics in Teesdale are often very bare but where disturbance is less extreme the surface can have a cover of the sedges of the variant, often with *Triglochin palustre* and some *Juncus alpinus*, and locally abundant *Cratoneuron commutatum* and *Drepanocladus revolvens*. In this scheme, this kind of fine variation is all accommodated in this variant: in Jones (1973) and Bradshaw & Jones (1976), it was described and mapped under different sub-variants in the *Pinguiculo-Caricetum*.

***Thymus praecox-Racomitrium lanuginosum* variant:** *Kobresieto-Caricetum* Ratcliffe 1965; *Caricetum lepidocarpae-hostianae kobresietosum* Shimwell 1968a; *Pinguiculo-Caricetum molinietosum* Wheeler 1975 p.p. This variant is floristically very similar to the last and in Upper Teesdale, where it is strongly centred, occurs in close association with it. But there are some obvious floristic differences. *Molinia* and *Eriophorum latifolium* are both very scarce and *Equisetum palustre*, *Triglochin palustre* and *Parnassia palustris* generally absent. *Sesleria* becomes rather uneven in its representation: it is absent from many stands (as in Ratcliffe's (1965) *Kobresieto-Caricetum*) but quite abundant in others (Jones 1973). The usual dominant, however, is *Kobresia*, with varying amounts of the sub-community sedges (though generally not much *C. dioica*) and, additionally here as a strong preferential, *C. capillaris*. More obviously, there is very frequently a little *Thymus praecox* and some scattered rosettes of *Plantago maritima*. *Thalictrum alpinum* is also preferential at lower frequency. Again, the ground is often rather hummocky in this variant and *Racomitrium lanuginosum* is often prominent on the raised areas. *Tortella tortuosa* and *Scapania aspera* have also been recorded from this vegetation.

***Gymnostomum recurvirostrum* sub-community:** Gravel flushes Pigott 1956a; *Gymnostometo-Caricetum* Ratcliffe 1965; *Pinguiculo-Caricetum equisetosum* Jones 1973 p.p. This very striking vegetation is superficially very different from other kinds of *Pinguiculo-Caricetum* but almost all the constants of the community are well represented, with only *Carex hostiana*, *C. pulicaris*, *Eriophorum angustifolium* and *Ctenidium moluscum* markedly reduced. Floristically, it is quite close to the *Briza-Primula* sub-community, with frequent records for *Festuca ovina*, *Linum catharticum*, *Primula farinosa*, *Thymus praecox*, *Agrostis stolonifera* and *Cratoneuron commutatum*, though *Carex flacca*, *Briza media*, *Triglochin palustris*, *Sesleria albicans* and *Parnassia palustris* are uncommon. Typically, though, it is not these vascular species, which are as a rule of low individual and total cover, that give the vegetation its

character. Much more obvious is the moss *Gymnostomum recurvirostrum*, which occurs occasionally in the *Briza-Primula* sub-community as a coloniser of eroding turf fragments and on patches of other bryophytes, but which here forms prominent hummocks, up to 30 cm high and 60 cm or so across. *Catascopium nigrum* can also be found occasionally forming smaller cushions.

Between these, there is characteristically much bare ground: eroding patches of soil, exposed rock debris and patches of accumulating wind-borne material. On these, the vascular plants form a generally fragmentary cover, representing remnants of once more continuous turf or areas of recolonisation. And some good preferentials of this variant are especially associated with these areas. *Plantago maritima* is very common but more strictly confined to such situations are *Sagina nodosa*, *Minuartia verna* and, in its only British locus, the very rare *M. stricta*, like the other two species a perennial of open conditions, but perhaps behaving as an annual (Coombe & White 1951, Pigott 1956a). *Juncus alpinus* and *J. triglumis* also tend to be better represented in these open areas than anywhere else in the community. Among the bryophytes, *Drepanocladus revolvens* and, especially nearer to the sources of springs, *Cratoneuron commutatum*, can also be abundant between the *Gymnostomum* hummocks. Recolonisation of the moss hummocks themselves can also sometimes be observed, as these break down with age and wind erosion, when some of the small sedges and rosette dicotyledons may gain a hold, particularly on the sheltered lee side and where the mounds have not been hardened by tufa-deposition (Pigott 1956a).

Again, both the hummocks and the intervening areas are here treated as part of a single vegetation type: in Jones (1973) and Bradshaw & Jones (1976) they were described and mapped separately as sub-variants.

Habitat

The *Pinguiculo-Caricetum* is typically a soligenous mire of mineral soils and shallow peats kept very wet by base-rich, calcareous and oligotrophic waters. It is predominantly a community of north-western Britain and the cool, wet climate of the region has an obvious influence on the floristics of the vegetation and, in more extreme situations, on the structure of the sward. However, most stands are grazed and trampled by large herbivores and it is probably these factors, combined with nutrient impoverishment and the often strong and scouring effect of the irrigation, which play the major part in maintaining the community in its generally rich, varied and open state.

The pH of the flushing waters here is high, usually between 5.5 and 7.0, sometimes higher (Poore 1955a, Pigott 1956a, McVean & Ratcliffe 1962, Birks 1973, Wheeler 1983) and the amount of dissolved calcium large, up to 100 mg l⁻¹ (Pigott 1956a, Wheeler 1983,

Wheeler *et al.* 1983), often with some re-precipitation as tufa among the herbage. These conditions are strongly reflected in the composition of the community which is one of the most calcicolous of our mires, much of its distinctive character being given by species such as *Carex dioica*, *C. hostiana*, *C. pulicaris*, *C. lepidocarpa*, *C. flacca*, *Sesleria albicans*, *Briza media*, *Eleocharis quinqueflora*, *Eriophorum latifolium*, *Linum catharticum* and *Tofieldia pusilla*, rarities like *Equisetum variegatum* and *Kobresia simpliciuscula*, and the bryophytes *Aneura pinguis*, *Drepanocladus revolvens*, *Campylium stellatum*, *Ctenidium molluscum*, *Cratoneuron commutatum*, *Gymnostomum recurvirostrum* and *Catascopium nigratum*. Such an assemblage provides a strong definition for the community against its counterparts in the Caricion nigrae and in flushed Oxycocco-Sphagneteta mires which occupy hydrologically similar, but more base-poor, situations.

Generally speaking, the source of base- and cation-enrichment here is calcareous bedrocks and superfcials, from which ground water emerges where it strikes impervious substrates, running down over the ground surface and through the upper soil horizons to create a slope flush. But these materials are quite varied in their lithology and occur in diverse geological settings. They include sedimentary limestones, notably the Carboniferous Limestone, which crops out in massive deposits in the Pennines with interbedded limy partings also occurring in the Yoredale transitions to the Millstone Grit (Holdgate 1955a, b, Pigott 1956a, Sinker 1960, Shimwell 1968a) and the Cambrian/Ordovician Durness Limestone which is of more local importance on Skye (Birks 1973) and the north-west Scottish mainland (McVean & Ratcliffe 1962). Elsewhere, the community can mark out percolation from occasional calcareous strata in such deposits as the Ordovician/Silurian shales of the Southern Uplands (e.g. Ferreira 1978). Then, it can occur over metamorphosed calcareous deposits, as in Upper Teesdale, where it is part of the complex of vegetation found over the 'sugar-limestone' (Pigott 1956a, 1978b, Ratcliffe 1965, Jones 1973) and in the Scottish Highlands, where it occurs widely on the Dalradian metasediments and, less commonly, those of the Moine series (Poore 1955a, McVean & Ratcliffe 1962). In Scotland, too, and in the Lake District, certain igneous rocks provide local enrichment of flushing waters. Very often, throughout its range, glacial superfcials, particularly fine-textured drift, make some contribution, ill-draining and calcareous, to the soil parent materials (Holdgate 1955a, Pigott 1956a, 1978b). The community can also be found on flushed shell-sand, as in some sites on the north Scottish coast (Ratcliffe 1977, Birse 1980), and on material redistributed by river erosion to which there has been a modest alluvial contribution (e.g. Pigott 1956a).

The soils which develop under the community in such diverse situations are often largely of mineral origin and, though the particular parent materials can be very different, the predominant influence of more or less continuous irrigation with lime-rich waters means that they can generally be classified as calcareous surface-water gleys (Soil Survey 1983). Typically, there is no stagnation and *in situ* formation of peat is very limited with usually no more than a humic topsoil, a feature which helps distinguish the habitat of the community from that of base-rich basins where it is replaced by vegetation like the *Carex-Calliergon* and *Carex-Sphagnum warnstorfi* mires in which swamp sedges play an important role, sometimes with more base-tolerant Sphagna, two groups of plants which are notably very scarce here. However, peat remnants can occur quite often, as where springs are eating back into tracts of blanket mire and, quite commonly, the community can be found on shallow peat surrounds to flushes, where irrigation occurs well within ombrogenous systems.

Variation in the degree of base- and cation-enrichment of the waters, the extent to which this effect is diffused as the waters emerge and the degree to which raised areas of the sward become removed from the immediate influence of irrigation, probably all play some part in the floristic differences between the various kinds of *Pinguiculo-Caricetum*, most obviously between the *Carex-Juncus* sub-community on the one hand and the *Briza-Primula* and *Gymnostomum* sub-communities on the other. The former, with its poorer representation of calcicoles and the preferential occurrence of species like *Carex demissa*, *Juncus bulbosus/kochii* and *Erica tetralix*, tends to occur more often on peaty gleys and shallow peats than the other types, and is predominantly a Scottish and Cumbrian vegetation type, marking out very local base-enrichment within the context of Nardogalion grasslands and Oxycocco-Sphagneteta wet heaths and mires on prevailingly acid soils. The latter types of *Pinguiculo-Caricetum*, with their more obvious calcicolous component, are usually found on surface-water gleys which are often little more than very wet lithomorphous soils, among tracts of calcicolous grasslands, most notably on the Pennine Carboniferous Limestone. But we need to know a great deal more about the ranges of edaphic variables here, about which are important and how their, perhaps quite subtle, control on the vegetation works (e.g. Poore 1955a, Clymo 1962, Wheeler *et al.* 1983).

Calcicolous flushes of the kind occupied by the *Pinguiculo-Caricetum* tend to occur more commonly towards the north-west of Britain, where suitable bedrocks and superfcials are widely, though often locally, distributed on the slopes of the upland fringes in a region with a wet and cool climate. Annual precipitation through the range of the community is almost always in

excess of 800 mm and usually more than 1200 mm (*Climatological Atlas* 1952) with typically more than 160 wet days yr^{-1} (Ratcliffe 1968), features which help maintain the constant flushing characteristic of the habitat. The generally low summer temperatures, with a mean annual maximum for the most part below 25 °C (Conolly & Dahl 1970), are also clearly reflected in the floristics of the community, with a good representation of Continental Northern plants like *Pinguicula vulgaris*, *Carex dioica*, *C. pulicaris* and *Eriophorum latifolium* and rarer species such as *Schoenus ferrugineus* and *Drosera anglica*, and the Northern Montane *Primula farinosa* and *Juncus alpinus*. In Scotland the community does not generally penetrate into high montane regions, but in the very harsh climate of Upper Teesdale, it provides a far-flung outpost for such Arctic-Alpine plants as *Kobresia*, *Tofieldia pusilla*, *Bartsia alpina*, *Carex capillaris*, *Juncus triglumis*, *Minuartia verna* and the only British locus for *M. stricta* (Pigott 1956a, Ratcliffe 1965). Towards the south-east of Britain, calcareous slope flushes are not unknown, but they are very local and, though similar vegetation can be found in this region, it lacks some of the most characteristic species of the community and, until further samples are available, its status must remain tentative. Certainly, at lower altitudes on flushed shell-sands, the *Pinguicula-Caricetum* closely approaches certain kinds of *Salix repens-Campyllum stellatum* dune-slack in its composition (e.g. Birse 1980). More generally in the lowland south-east, with its warmer and drier climate, the community is replaced by the *Schoenetum nigricantis*, though this vegetation type extends on to deeper base-rich peats of valley mires and some basin mires. The *Cirsium palustre* variant of the *Briza-Primula* sub-community shows some strong affinities with that community and with those Molinietalia fen-meadows that occupy fairly base-rich sites with a higher nutrient turnover than is usual in the habitat of the *Pinguicula-Caricetum*, which is very typically of low productivity with little nitrogen and phosphorus in the profile, a feature of great importance in maintaining the open and often sedge-dominated character of the sward (Pigott 1956a, 1978b; Wheeler 1983, Wheeler *et al.* 1983).

Although bulkier dominants like *Schoenus* or *Molinia*, and a variety of taller fen herbs, can make some prominent contribution to the cover in this *Cirsium* variant and other kinds of *Pinguicula-Caricetum*, the herbage of this kind of mire is much more commonly kept very short because of grazing. Throughout its range, the community typically occurs in unenclosed uplands to which, in summer, stock have free access: generally, sheep are the predominant grazers but in some sites cattle and ponies are important and, in Scotland especially, deer. The constant nibbling of the turf, which in early summer can yield a good bite

because of the irrigation, undoubtedly contributes to the richness of the sward and the great diversity in dominance in the community, by helping keep more vigorous species in check.

But there is a further effect of herbivores which is of great importance in controlling the physiognomy of the vegetation and the openness of the ground, and that is trampling (Pigott 1956a). On the generally very wet surfaces here, this tends to disrupt the sward and contributes to maintaining the turf in an irregular and discontinuous condition, with patches of exposed and redistributed mineral and organic matter and even bare bedrock fragments or drift. Flushing itself can play a large part in the erosion of the surface, particularly where the sward has already been broken. Sometimes the community marks out sites of rather diffuse irrigation below weak spring lines or where waters percolate some distance beneath a soil mantle; but more vigorous flushing, augmented in areas of harsher climate by snow-melt, and working more obviously on steeper slopes, can scour these flushes, washing away substantial amounts of soil and leaving systems of bare runnels and flats between irregular fragments of perched vegetation. Wind ablation of these blocks can undercut them and cause collapse and, where the winters are harsh, freeze-thaw can burst open the remnants of the sward and intervening areas of debris, causing further loosening of the surface. Strong flushes can also eat back upslope, enlarging the potential area of occupation of the community and feeding the process of redistribution of soil and rock. Such effects have been observed in many flushes of this kind (e.g. Holdgate 1955a, Birks 1973, Wheeler *et al.* 1983), and they contribute generally to a horizontal and vertical differentiation of intimately juxtaposed microhabitats. But they are especially well seen in Upper Teesdale, where a harsh climate and intensive trampling by stock are actively eroding flushed slopes of sugar-limestone, much of which has already been well disintegrated under a mantle of drift and peat, and creating a unique complex of variants of the *Pinguicula-Caricetum*, pictured very clearly in the profiles of Pigott (1956a) and the maps of Bradshaw & Jones (1976). The *Briza-Primula* sub-community occupies most of the ground in these flushes (though there are areas which are close to the *Carex-Juncus* sub-community); the *Thymus-Racomitrium* variant is on the drier areas, the *Molinia-Eriophorum* on the wetter. And, in the most open places, there are some striking stands of the *Gymnostomum* sub-community which seems essentially to represent a regeneration vegetation, colonising fragments of existing sward, eroded soil material or accumulated aeolian detritus, offering a temporary site for invasion by vascular plants, and then declining as the hummocks open up and decay (Pigott 1956a, Ratcliffe 1965).

Zonation and succession

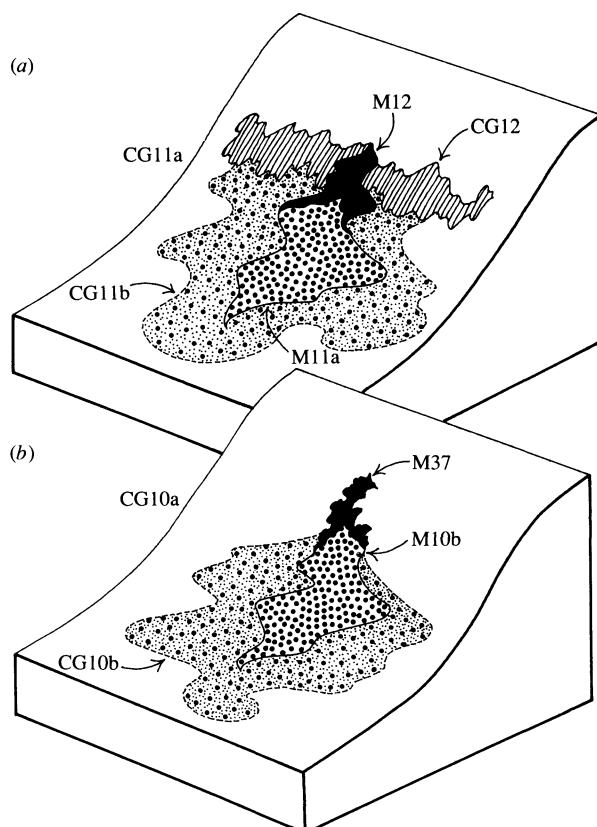
The *Pinguiculo-Caricetum* marks out areas of soligenous influence of base-rich and calcareous waters, often in association with spring and rill vegetation, within grasslands and more occasionally in ombrogenous mires and around topogenous mires. Stands are usually small and their definition in zonations depends on the strength of flushing and the degree of base-enrichment. Most stands

are affected by herbivores and some would probably progress to *Alno-Ulmion* scrub or woodland if grazing were withdrawn; at higher altitudes, the vegetation may be a climatic climax, though with an internally dynamic character.

The most widespread situation in which the community occurs is within sub-montane pastures where it typically forms a zone below springs and flush-lines, often pear-shaped and elongated downslope below isolated sites of irrigation, in larger stands of more complex configuration where flushing is extensive. Towards the source of flushing it commonly gives way to *Cratoneuron* spring vegetation, usually the *Cratoneuron-Festuca rubra* community which can extend as a narrow strip down a central vigorous rill. In Scotland especially but also in the Lake District and more locally in the Pennines, *Saxifraga aizoides* rises to prominence in the continuously splashed zone to the centre of these flushes and there is frequently a clear intervening band of the *Carici-Saxifragetum* (McVean & Ratcliffe 1962, Birks 1973). Where the waters are somewhat less base-rich, the spring vegetation may be represented by the *Cratoneuron-Carex nigra* community, particularly towards higher altitudes in Scotland, where this vegetation type subsumes part of McVean & Ratcliffe's (1962) *Hypno-*

Figure 14. Base-rich flushes among pasture at high (a) and moderate (b) altitudes in northern Britain.

- M10b *Pinguiculo-Caricetum* mire, *Briza-Primula* sub-community
- M11a *Carici-Saxifragetum* mire, *Thalictrum-Juncus* sub-community
- M12 *Caricetum saxatilis* mire
- M37 *Cratoneuron-Festuca* spring
- CG10a *Festuca-Agrostis-Thymus* grassland, *Trifolium-Luzula* sub-community
- CG10b *Festuca-Agrostis-Thymus* grassland, *Carex* sub-community
- CG11a *Festuca-Agrostis-Alchemilla* grass-heath, Typical sub-community
- CG11b *Festuca-Agrostis-Alchemilla* grass-heath, *Carex* sub-community
- CG12 *Festuca-Alchemilla-Silene* dwarf-herb community



Caricetum alpinum, or even by some kind of *Philonotis* flush where the waters are only weakly calcareous (Holdgate 1955a, Pigott 1956a). Where flushing occurs on more level ground, complex mosaics of these communities can be seen around the springs (e.g. Poore 1955a, McVean & Ratcliffe 1962).

Towards the margins of these flushes, the *Pinguiculo-Caricetum* gives way, with varying degrees of abruptness, to the pasture vegetation on drier ground, often standing out in the smooth swards, by virtue of its uneven and broken surface. In Scotland, where the community is generally represented by the *Carex-Juncus* sub-community, a very widespread context for the *Pinguiculo-Caricetum* is the *Festuca-Agrostis-Thymus* grassland, the common plagioclimax sward of more base-rich brown earths associated with local calcareous outcrops in the Dalradian and, less so, the Moine Assemblages and the Durness Limestone of the far north-west (McVean & Ratcliffe 1962, Birks 1973, Ratcliffe 1977). In the Lake District, a similar zonation can be seen on more calcareous parts of the Borrowdale Volcanics. In Scotland, too, in situations where the surrounding soils are somewhat less base-rich, the *Pinguiculo-Caricetum* can occur within stretches of the *Festuca-Agrostis-Alchemilla* grass-heath. In both of these grassland types, a *Carex pulicaris-Carex panicea* sub-community often forms a transition zone on the mildly-irrigated surrounds to the flush (Figure 14) but more abrupt zonations can occur and where soligenous base-enrichment is very localised within stretches of more prevailingly pervious and acidic rocks and soils, the *Pinguiculo-Caricetum* may be very sharply marked off from calcifugous *Festuca-Agrostis* grassland.

Comparable zonations to the above can be found in the northern Pennines, though here the *Briza-Primula* sub-community is the usual kind of *Pinguiculo-Caricetum* and the pasture is generally the *Sesleria-Galium* grassland. With the more uniformly calcareous condition of the soils over the Carboniferous Limestones, there is often a very strong floristic continuity between the different vegetation types, the axis of variation being largely controlled by the amount of soil moisture. A common sequence is from the Typical sub-community of the grassland, through (again) a *Carex pulicaris-Carex panicea* sub-community and then to the *Molinia-Eriophorum* variant of the mire, species such as *Sesleria*, *Festuca ovina*, *Carex flacca*, *Briza media* and *Linum catharticum* running throughout with virtually undiminished frequency. In Upper Teesdale, the presence of species such as *Kobresia*, *Carex capillaris*, *Plantago maritima* and *Racomitrium uliginosum* enriches both the pasture (often represented by its *Carex-Kobresia* sub-community) and the drier parts of the mire (in the *Thymus-Racomitrium* variant) in this kind of zonation and the *Gymnostomum* sub-community appears on the

open gravels (Pigott 1956a, Ratcliffe 1965, Jones 1973, Bradshaw & Jones 1976). Sadly, some of the most intricate of these patterns were lost beneath the Cow Green reservoir. More locally in northern England and north Wales, the *Briza-Primula* sub-community can pick out flushes within the *Festuca-Avenula* grassland or, in Durham, the *Sesleria-Scabiosa* grassland.

Less common than these kinds of situation, though often very striking because of the close juxtaposition of rather different vegetation types, are those occurrences of the *Pinguiculo-Caricetum* around places of soligenous base-enrichment within ombrogenous mires. Fragments of perched blanket mire can sometimes be found where springs are biting back on to gentle peat-clad slopes above (as in upper Teesdale: Pigott 1956a) but, in Scotland, the *Carex-Juncus* sub-community can occur in prevailing ombrogenous systems, particularly at lower altitudes in the west, where it gives way directly to the *Scirpus-Eriophorum* mire or sometimes to an intervening zone of the *Carex panicea* sub-community of the *Scirpus-Erica* wet heath, into which *C. panicea*, *C. pulicaris*, *C. echinata*, *C. demissa*, *Pinguicula vulgaris*, *Selaginella selaginoides* and locally dominant *Schoenus nigricans* extend their cover (Poore 1955a, McVean & Ratcliffe 1962). In this kind of setting, and where the *Pinguiculo-Caricetum* occurs more locally in stretches of heath on thin, dry peats, the community typically stands out as fresh green patches.

Although the flushes with which this kind of mire is associated are often isolated (though repeated) on slopes, they sometimes feed topogenous fens in basins or channels and then the *Pinguiculo-Caricetum* can form a fringing zone around the central area, passing to communities like the *Carex-Calliergon* mire or, more exclusively at higher altitudes, the *Carex-Sphagnum warnstorffii* mire on the deeper peat of the more stagnant waters. Such transitions are well seen in small hollows in the central Highlands (McVean & Ratcliffe 1962), where the *Carex-Juncus* sub-community forms the margins, and at Sunbiggin Tarn (Holdgate 1955a) and Malham Tarn (Sinker 1960, Proctor 1974), where the *Briza-Primula* sub-community occurs.

Almost throughout its range, the *Pinguiculo-Caricetum* is strongly affected by grazing animals. Without such influence, many stands would probably be open to invasion by shrubs and trees though nutrient deficiency in the soils might be an important hindrance to some species. Likely colonisers are *Betula pubescens*, *Salix cinerea* and, in these northern localities, *S. pentandra*, *S. phylicifolia*, *S. nigricans* and *Prunus padus* with *Fraxinus excelsior* figuring on drier margins; *Alnus glutinosa* is more problematic because of the difficulty of fruit transport. Such mixtures are most characteristic of our Alno-Ulmion woodlands like the *Alnus-Fraxinus-Lysimachia* woodland and wetter stands of the *Fraxinus-*

Sorbus-Mercurialis woodland, beneath the canopies of which there is often a good representation of the kinds of tall herbs that figure in the *Cirsium palustre* variant here. In some localities, as in Teesdale and Weardale in Durham and in Swaledale in North Yorkshire, small patches of *Pinguicula-Caricetum* persist in the wetter parts of traditionally-treated hay-meadows, whose vegetation has probably been secondarily derived from these kinds of forest (Pigott 1956a).

Distribution

The community is of widespread but local occurrence throughout northern England and Scotland with fragmentary and often rather impoverished stands in Wales and the Midlands. The *Carex-Juncus* sub-community is largely restricted to Scotland and the Lake District with outlying occurrences in north Wales and Upper Teesdale, the *Schoenus* variant confined to low altitudes, the other variants extending to higher levels. The *Briza-Primula* sub-community is the predominantly northern England type, being centred on the Pennines where the *Molinia-Eriophorum* variant is the common expression, but also including species-poor stands and the transitional vegetation of the *Cirsium* variant further south. The *Thymus-Racomitrium* variant and the *Gymnostomum* sub-community have been described only from Upper Teesdale.

Affinities

The *Pinguicula-Caricetum* as defined here is an expanded version of the community given that name by Jones (1973: see also Bradshaw & Jones 1976) and amended by Wheeler (1975, 1980b), taking in a variety of other vegetation types with essentially similar floristics, most notably the Scottish flushes first described by Poore (1955a) and McVean & Ratcliffe (1962) and later by Birse (1980, 1984: see also Birse & Robertson 1976). Although quite diverse in its composition and structure, it is well defined against most of the closely-related mires and its floristic affinities are fairly straightforward.

Through the *Carex-Juncus* sub-community it grades to soligenous Caricion *nigrae* poor fens and some Oxy-cocco-Sphagnetum vegetation of more base-poor flushes, like the *Carex-Nardus* sub-community of the *Carex echinata-Sphagnum* mire and the *Carex panicea* sub-community of the *Scirpus-Erica* wet heath. *Molinia*, *Eriophorum angustifolium* and some of the more broadly-tolerant small sedges or plants like *Erica tetralix* and *Juncus bulbosus/kochii* provide links in this direction, but the great predominance of calcicoles here and the consistent replacement of Sphagna by brown mosses provide good diagnostic features. Through the *Briza-Primula* sub-community, the community shows a strong continuity with Mesobromion swards, notably the *Sesleria-Galium* grassland, and richer Nardo-Galion

communities like the *Festuca-Agrostis-Thymus* grassland, reflecting the impact of grazing over drier areas differentiated in the flushed sward: here the calcicolous or mesophytic element is maintained throughout the sequence, the proportion of hydrophilous species providing the major distinction. Affinities with Molinietales communities can be seen locally but these are much more obvious in the *Schoenetum* which replaces this community, with some floristic transitions, towards the southern lowlands of Britain.

Transitions to spring and rill vegetation of the Cardamino-Montion and Cratoneurion alliances are a little more difficult to define, particularly in Scotland and the Lake District where *Saxifraga aizoides* provides a strong link between the two: the closest community to the *Pinguicula-Caricetum* is the *Carici-Saxifragetum aizoidis* with which it shares many calcicolous herbs and bryophytes.

In phytosociological terms, this is our central Caricion davallianae small-sedge mire, showing clear affinities, particularly through the *Briza-Primula* sub-community, with communities like the *Caricetum davallianae* Dutoit 1924 *emend.* Görs 1963 described from Germany (Görs 1964, Oberdorfer 1977, Ellenberg 1978), Switzerland (Dutoit 1924) and Poland (Matuszkiewicz 1981) and the *Parnassio-Caricetum pulicaris* (Oberdorfer 1957) Görs 1963 and *Pinguicula-Parnassietum* (Libbert 1928) Passarge 1964 described from Germany (Görs 1963, Passarge 1964) and The Netherlands (Westhoff & den Held 1969). Through higher-altitude stands in this sub-community and also through the *Carex-Juncus* type, there are also links with the Scandinavian base-rich mires, like the Braunmos-reiche *Carex panicea* Assoziation (Nordhagen 1928), generally placed in the Caricion bicolori-atrofuscae (Nordhagen 1928, 1943; see also Persson 1961, Svensson 1965, Hallberg 1971, Ellenberg 1978): such communities, however, often have a good representation of Arctic-Alpine willows, best seen in Britain in ungrazed wet tall-herb vegetation and high-altitude scrub. The *Schoenus* variant also includes vegetation which, on mainland Europe, has been placed in a variety of *Schoeneta*, like the *Orchio-Schoenetum nigricantis* Oberdorfer 1957 described from Germany (Oberdorfer 1957, 1977) and Poland (Matuszkiewicz 1981). *S. ferrugineus* figures much more extensively in these communities on the Continent, notably in the alpine foothills (as in the *Primulo-Schoenetum ferruginei* (Koch 1926), Oberdorfer (1957) 1962) and around the Baltic, and Nordhagen (1937) placed low-productivity, base-rich mires from low altitudes in an alliance *Schoenion ferruginei* (Wheeler *et al.* 1983: see also Görs 1964, Kloss 1965, Tyler 1979). British *Schoenus* flushes in the *Pinguicula-Caricetum* have a distinctly oceanic character compared with European *Schoeneta* of this kind.

Floristic table M10

	a	b	c	10
<i>Carex panicea</i>	V (1–5)	V (1–6)	V (1–7)	V (1–7)
<i>Pinguicula vulgaris</i>	V (1–5)	IV (1–3)	IV (1–4)	V (1–5)
<i>Carex dioica</i>	III (1–6)	IV (1–5)	V (1–5)	IV (1–6)
<i>Aneura pinguis</i>	III (1–5)	IV (1–4)	IV (1–4)	IV (1–5)
<i>Drepanocladus revolvens</i>	III (1–9)	IV (1–7)	IV (2–7)	IV (1–9)
<i>Juncus articulatus</i>	III (1–5)	IV (1–4)	IV (1–3)	IV (1–5)
<i>Carex lepidocarpa</i>	II (1–6)	IV (1–6)	IV (2–5)	IV (1–6)
<i>Bryum pseudotriquetrum</i>	II (1–5)	IV (1–3)	IV (1–2)	IV (1–5)
<i>Campylium stellatum</i>	V (1–7)	IV (1–4)	II (2–4)	IV (1–7)
<i>Selaginella selaginoides</i>	III (1–5)	IV (1–4)	II (2–4)	III (1–5)
<i>Carex hostiana</i>	IV (1–7)	V (1–6)		IV (1–7)
<i>Ctenidium molluscum</i>	III (1–9)	V (1–8)	I (2)	IV (1–8)
<i>Carex pulicaris</i>	III (1–6)	IV (1–5)		IV (1–6)
<i>Eriophorum angustifolium</i>	III (1–7)	IV (1–4)		IV (1–7)
<i>Potentilla erecta</i>	III (1–5)	IV (1–6)		III (1–6)
<i>Succisa pratensis</i>	III (1–6)	IV (1–4)		III (1–6)
<i>Molinia caerulea</i>	III (1–7)	IV (1–6)		III (1–7)
<i>Carex nigra</i>	III (1–7)	III (1–4)	I (1–3)	III (1–7)
<i>Fissidens adianthoides</i>	II (1–5)	III (1–3)		II (1–5)
<i>Anthoxanthum odoratum</i>	II (1–7)	II (1–3)		II (1–7)
<i>Ditrichum flexicaule</i>	I (1–3)	I (1–3)		I (1–3)
<i>Thalictrum alpinum</i>	I (1–5)	I (1–3)		I (1–5)
<i>Hylocomium splendens</i>	I (1–7)	I (1–3)		I (1–7)
<i>Sphagnum subnitens</i>	I (1–3)	I (1)		I (1–3)
<i>Ranunculus acris</i>	I (1–4)	I (1–3)		I (1–4)
<i>Taraxacum officinale</i> agg.	I (1–3)	I (1–3)		I (1–3)
<i>Festuca ovina</i>	II (1–5)	III (1–7)	III (2–4)	II (1–7)
<i>Linum catharticum</i>	I (1–3)	IV (1–4)	III (1–2)	II (1–4)
<i>Primula farinosa</i>	I (1–5)	IV (1–4)	III (1–3)	II (1–4)
<i>Cratoneuron commutatum</i>	I (1–5)	III (1–6)	IV (1–4)	II (1–6)
<i>Agrostis stolonifera</i>	I (1)	III (1–3)	IV (1–4)	II (1–4)
<i>Thymus praecox</i>	I (1)	II (1–4)	III (1–2)	II (1–4)
<i>Equisetum variegatum</i>	I (1–3)	II (1–6)	II (1–3)	I (1–6)
<i>Juncus alpinus</i>	I (1–5)	II (1–3)	II (1–2)	I (1–5)
<i>Cratoneuron filicinum</i>		I (1–3)	I (2–3)	I (1–3)
<i>Deschampsia cespitosa</i>		I (1–4)	I (3)	I (1–4)
<i>Eleocharis quinqueflora</i>	III (1–7)	II (1–4)	II (1–4)	III (1–7)
<i>Carex demissa</i>	III (1–9)	I (1–3)	I (1–3)	III (1–9)
<i>Juncus bulbosus/kochii</i>	III (1–6)	I (1–3)		II (1–6)
<i>Erica tetralix</i>	III (1–7)	I (1–4)		II (1–7)
<i>Scorpidium scorpioides</i>	III (1–8)	I (1)		II (1–8)
<i>Carex echinata</i>	II (1–7)	I (1–3)		II (1–7)
<i>Narthecium ossifragum</i>	II (1–5)	I (1–3)		I (1–5)
<i>Drosera rotundifolia</i>	II (1–5)	I (1)		I (1–5)
<i>Saxifraga aizoides</i>	II (1–5)	I (2–5)		I (1–5)

Floristic table M10 (*cont.*)

	a	b	c	10
<i>Schoenus nigricans</i>	II (2–5)	I (1)		I (1–5)
<i>Polygonum viviparum</i>	I (1–4)			I (1–4)
<i>Juncus squarrosus</i>	I (1–5)			I (1–5)
<i>Scirpus cespitosus</i>	I (1–5)			I (1–5)
<i>Pedicularis sylvatica</i>	I (1–3)			I (1–3)
<i>Drosera anglica</i>	I (1–5)			I (1–5)
<i>Blindia acuta</i>	I (1–3)			I (1–3)
<i>Schoenus ferrugineus</i>	I (1–10)			I (1–10)
<i>Myrica gale</i>	I (1–5)			I (1–5)
<i>Pinguicula lusitanica</i>	I (1–5)			I (1–5)
<i>Breutelia chrysocoma</i>	I (1–3)			I (1–3)
<i>Triglochin palustris</i>	II (1–4)	IV (1–3)	II (1)	III (1–4)
<i>Carex flacca</i>	II (1–6)	IV (1–5)	I (3)	II (1–5)
<i>Briza media</i>	I (1–6)	IV (1–4)		II (1–4)
<i>Racomitrium lanuginosum</i>	I (1–4)	III (1–9)	II (1–2)	II (1–9)
<i>Prunella vulgaris</i>	I (1–6)	III (1–6)	I (2–4)	II (1–6)
<i>Parnassia palustris</i>	I (1–3)	III (1–3)	I (2)	II (1–5)
<i>Equisetum palustre</i>	II (1–5)	III (1–4)		II (1–5)
<i>Eriophorum latifolium</i>	II (1–8)	III (1–4)		II (1–8)
<i>Kobresia simpliciuscula</i>		III (2–8)	II (1–2)	II (1–8)
<i>Leontodon autumnalis</i>	I (1–5)	III (1–3)		I (1–5)
<i>Tofieldia pusilla</i>	I (1–3)	II (1–4)	I (1)	I (1–4)
<i>Calliergon cuspidatum</i>	I (1–8)	II (1–4)		I (1–8)
<i>Pellia endiviifolia</i>	I (1–5)	II (1–3)		I (1–5)
<i>Pedicularis palustris</i>	I (1–3)	II (1–4)		I (1–4)
<i>Filipendula ulmaria</i>	I (5)	II (1–3)		I (1–5)
<i>Ranunculus flammula</i>	I (1–4)	II (1–3)		I (1–4)
<i>Cirsium palustre</i>	I (1–3)	II (1–3)		I (1–3)
<i>Cardamine pratensis</i>	I (1)	II (1–3)		I (1–3)
<i>Leontodon taraxacoides</i>		II (1–4)		I (1–4)
<i>Sesleria albicans</i>		II (1–7)		I (1–7)
<i>Valeriana dioica</i>		II (1–3)		I (1–3)
<i>Angelica sylvestris</i>		II (1–3)		I (1–3)
<i>Galium uliginosum</i>		II (1–3)		I (1–3)
<i>Plagiomnium rostratum</i>		II (1–3)		I (1–3)
<i>Tortella tortuosa</i>		I (2–3)		I (2–3)
<i>Scapania aspera</i>		I (1–3)		I (1–3)
<i>Bartsia alpina</i>		I (2–3)		I (2–3)
<i>Caltha palustris</i>		I (1–3)		I (1–3)
<i>Juncus acutiflorus</i>		I (1–4)		I (1–4)
<i>Luzula multiflora</i>		I (1–3)		I (1–3)
<i>Dactylorhiza fuchsii</i>		I (1–3)		I (1–3)
<i>Holcus lanatus</i>		I (1–3)		I (1–3)
<i>Galium palustre</i>		I (1–3)		I (1–3)

<i>Plantago maritima</i>	I (1–5)	II (1–4)	IV (1–3)	II (1–5)
<i>Gymnostomum recurvirostrum</i>		I (2–4)	V (1–10)	I (1–10)
<i>Sagina nodosa</i>		I (1–3)	III (1–3)	I (1–3)
<i>Minuartia verna</i>			III (2–4)	I (2–4)
<i>Carex capillaris</i>	I (1–3)	I (1–4)	II (1–4)	I (1–4)
<i>Juncus triglumis</i>	I (1–2)	I (1–3)	II (2–3)	I (1–3)
<i>Catascopium nigrum</i>			II (2–5)	I (2–5)
<i>Minuartia stricta</i>			I (1–2)	I (1–2)
<i>Euphrasia officinalis</i> agg.	II (1–5)	III (1–4)	II (1–2)	II (1–5)
<i>Nardus stricta</i>	I (1–7)	I (1–4)	I (2)	I (1–7)
<i>Festuca rubra</i>	I (1–5)	I (1–5)	I (1–2)	I (1–5)
Number of samples	143	55	19	217
Number of species/sample	23 (11–49)	37 (19–56)	21 (10–29)	25 (10–56)
Herb height (cm)	13 (4–35)			
Herb cover (%)	76 (20–100)	77 (50–100)	36 (20–50)	74 (20–100)
Bryophyte height (mm)	16 (2–30)			
Bryophyte cover (%)	45 (2–95)	58 (30–90)	65 (25–100)	49 (2–100)
Altitude (m)	269 (1–792)			
Slope (°)	8 (0–30)	6 (0–20)	2 (0–5)	7 (0–30)
Soil pH	6.6 (5.8–7.2)			

a *Carex demissa*-*Juncus bulbosus*/kochii sub-community

b *Briza media*-*Primula farinosa* sub-community

c *Gymnostomum recurvirostrum* sub-community

10 *Pinguiculo-Caricetum dioicae* (total)

Floristic table M10, variants

	ai	aII
<i>Carex panicea</i>	V (1–9)	V (1–7)
<i>Pinguicula vulgaris</i>	V (1–4)	IV (1–5)
<i>Campylium stellatum</i>	V (1–7)	V (1–9)
<i>Carex dioica</i>	III (1–6)	II (1–6)
<i>Aneura pinguis</i>	III (1–5)	III (1–4)
<i>Drepanocladus revolvens</i>	III (1–9)	III (1–7)
<i>Juncus articulatus</i>	III (1–3)	III (1–5)
<i>Carex lepidocarpa</i>	II (1–6)	II (1–6)
<i>Bryum pseudotriquetrum</i>	II (1–5)	III (1–4)
<i>Selaginella selaginoides</i>	III (1–3)	IV (1–3)
<i>Carex pulicaris</i>	III (1–5)	V (1–6)
<i>Eriophorum angustifolium</i>	V (1–7)	IV (1–5)
<i>Potentilla erecta</i>	III (1–5)	III (1–5)
<i>Carex nigra</i>	III (1–7)	III (1–5)
<i>Molinia caerulea</i>	II (1–5)	III (1–7)
<i>Succisa pratensis</i>	II (1–3)	IV (1–6)
<i>Carex hostiana</i>	II (1–6)	IV (1–7)
<i>Ctenidium molluscum</i>	I (1–5)	IV (1–9)
<i>Fissidens adianthoides</i>	I (1–5)	IV (1–5)
<i>Eleocharis quinqueflora</i>	IV (1–7)	II (1–7)
<i>Carex demissa</i>	III (1–7)	II (1–9)
<i>Juncus bulbosus/kochii</i>	III (1–6)	III (1–5)
<i>Erica tetralix</i>	II (1–5)	III (1–7)
<i>Scorpidium scorpioides</i>	III (1–8)	II (1–8)
<i>Carex echinata</i>	II (1–5)	II (1–7)
<i>Narthecium ossifragum</i>	II (1–4)	I (1–5)
<i>Drosera rotundifolia</i>	I (1–5)	II (1–3)
<i>Saxifraga aizoides</i>	I (1–3)	II (1–5)
<i>Polygonum viviparum</i>	I (1–3)	II (1–4)
<i>Juncus squarrosus</i>	I (1–3)	I (1–5)
<i>Scirpus cespitosus</i>	I (1–5)	I (1–3)
<i>Pedicularis sylvatica</i>	I (1–3)	I (1–3)

aiii	bi	bii	biii
V (1-5)	V (1-4)	V (1-5)	V (1-6)
V (1-5)	V (1-3)	IV (1-3)	III (1-3)
V (1-7)	IV (1-4)	IV (1-4)	IV (1-4)
III (1-5)	III (1-4)	V (1-4)	IV (1-5)
II (1-3)	IV (1-3)	IV (1-3)	III (1-4)
III (1-5)	III (1-4)	IV (1-7)	IV (1-4)
II (1-5)	IV (1-4)	IV (1-4)	IV (1-3)
I (1-5)	IV (1-6)	IV (1-4)	IV (1-4)
I (1-3)	V (1-3)	IV (1-3)	III (1-3)
III (1-5)	II (1-3)	IV (1-3)	V (1-4)
II (1-3)	IV (1-3)	IV (1-5)	IV (1-5)
II (1-3)	III (1-3)	IV (1-4)	III (1-4)
II (1-3)	III (1-3)	IV (1-6)	IV (1-4)
III (1-5)	IV (1-3)	III (1-4)	II (1-3)
IV (1-5)	V (1-6)	V (1-5)	I (1)
III (1-3)	V (1-3)	IV (1-4)	I (1-3)
IV (1-5)	V (1-6)	V (1-5)	IV (1-5)
II (1-5)	IV (1-3)	V (1-6)	V (2-8)
I (1-3)	III (1-3)	IV (1-3)	III (1-3)
III (1-7)	III (1-4)	II (1-4)	II (1-4)
III (1-5)		I (1-3)	I (1-3)
III (1-5)		II (1-3)	
IV (1-5)	II (1-3)	I (1-4)	I (1-2)
V (1-7)	I (1)		
III (1-5)	II (1-3)	I (1-2)	I (1-2)
III (1-5)		I (1-3)	
III (1-3)	I (1)		
II (1-5)		I (2-5)	I (2-5)
I (1)			
II (1-5)			
I (1-3)			

Schoenus nigricans
Drosera anglica
Blindia acuta
Pinguicula lusitanica
Myrica gale
Schoenus ferrugineus
Breutelia chrysocoma

<i>Briza media</i>	I (1–6)	I (1–4)
<i>Carex flacca</i>	I (1–5)	II (1–6)
<i>Linum catharticum</i>	I (1–3)	II (1–3)
<i>Cratoneuron commutatum</i>	I (1–5)	II (1–5)
<i>Prunella vulgaris</i>	I (1–4)	II (1–5)
<i>Primula farinosa</i>		
<i>Euphrasia officinalis</i> agg.	II (1–4)	III (1–5)
<i>Leontodon autumnalis</i>	I (1–3)	II (1–5)
<i>Agrostis stolonifera</i>	I (1)	
<i>Equisetum palustre</i>	III (1–5)	II (1–3)
<i>Triglochin palustris</i>	II (1–3)	II (1–4)
<i>Parnassia palustris</i>	I (1)	II (1–3)
<i>Festuca ovina</i>	I (1–5)	III (1–5)
<i>Equisetum variegatum</i>	I (1–3)	
<i>Sesleria albicans</i>		
<i>Juncus alpinus</i>	I (1–3)	I (1–5)
<i>Tofieldia pusilla</i>	I (1–3)	I (1–3)
<i>Juncus triglumis</i>	I (1)	I (2)
<i>Calliergon cuspidatum</i>	I (1–4)	II (1–8)
<i>Cirsium palustre</i>		I (1–3)
<i>Cardamine pratensis</i>		I (1)
<i>Valeriana dioica</i>		
<i>Filipendula ulmaria</i>		
<i>Angelica sylvestris</i>		
<i>Galium uliginosum</i>		
<i>Plagiomnium rostratum</i>		
<i>Cratoneuron filicinum</i>		
<i>Menyanthes trifoliata</i>		

V (2-5)	I (1)		
IV (1-5)			
III (1-3)			
II (1-5)			
II (1-5)			
I (1-10)			
I (1-3)			
<hr/>			
	IV (1-3)	IV (1-3)	IV (1-4)
II (1-5)	IV (1-4)	IV (1-4)	III (1-5)
I (1)	III (1-3)	IV (1-4)	IV (1-3)
I (1-3)	IV (1-6)	III (1-5)	III (1-4)
I (1)	III (1-3)	III (1-3)	IV (1-6)
	II (1-3)	IV (1-3)	IV (1-4)
I (1-3)	III (1-3)	III (1-4)	IV (1-3)
	III (1-3)	III (1-3)	II (2-3)
	III (1-3)	III (1-3)	II (1-2)
<hr/>			
I (5)	IV (1-3)	IV (1-4)	
II (1-3)	V (1-3)	IV (1-3)	
	IV (1-3)	IV (1-3)	I (3)
I (1-5)	I (1)	IV (1-6)	IV (2-7)
	I (1)	III (1-6)	III (1-4)
		III (1-4)	III (2-7)
I (1-3)		II (1-2)	II (1-3)
I (1)		II (1-3)	II (2-4)
		I (1-3)	I (1-3)
<hr/>			
I (1)	V (1-4)	III (1-3)	I (2)
	V (1-3)	I (1)	
	IV (1-3)	I (1-3)	
	IV (1-3)	II (1-3)	
I (5)	IV (1-3)		
	IV (1-3)		
	IV (1-3)		
	IV (1-3)		
	III (1-3)	I (1-3)	I (1-2)
II (1-5)	III (1-4)		

Floristic table M10, variants (*cont.*)

	ai	aii
<i>Carex rostrata</i>		
<i>Luzula multiflora</i>		
<i>Caltha palustris</i>		
<i>Juncus acutiflorus</i>		
<i>Dactylorhiza fuchsii</i>		
<i>Holcus lanatus</i>		
<i>Galium palustre</i>		
<i>Eriophorum latifolium</i>	I (2)	I (1–6)
<i>Leontodon taraxacoides</i>		
<i>Pellia endiviifolia</i>	I (5)	I (1–3)
<i>Scapania aspera</i>		
<i>Bartsia alpina</i>		
<i>Thymus praecox</i>	I (1)	
<i>Racomitrium lanuginosum</i>		I (1–4)
<i>Kobresia simpliciuscula</i>		
<i>Plantago maritima</i>	I (1–2)	I (1–5)
<i>Carex capillaris</i>	I (1–3)	
<i>Thalictrum alpinum</i>	I (1–5)	I (1–5)
<i>Ditrichum flexicaule</i>		I (1–3)
<i>Tortella tortuosa</i>		
<i>Anthoxanthum odoratum</i>	II (1–7)	II (1–4)
<i>Ranunculus flammula</i>	II (1–4)	I (1–3)
<i>Pedicularis palustris</i>	I (1–3)	I (1–3)
<i>Festuca rubra</i>	I (1–3)	II (1–5)
<i>Nardus stricta</i>	I (1–5)	II (1–7)
<i>Hylocomium splendens</i>	I (1)	II (1–7)
<i>Ranunculus acris</i>	I (1–3)	I (1–4)
<i>Taraxacum officinale</i> agg.	I (1–3)	I (1–3)
<i>Sphagnum subnitens</i>	I (1–3)	

aiii	bi	bii	biii
II (1-7)	III (1-3) III (1-3) III (1-3) III (1-4) III (1-3) III (1-3) III (1-3)		
III (1-8)	II (1-4) II (1-3)	IV (1-4) III (1-4)	I (1)
I (1)	II (1-3)	II (1-2) I (1-3) I (2-3)	I (2) I (1-3) I (2)
I (1)		II (1-4) I (1-4) II (2-6)	IV (1-4) IV (1-9) IV (2-8)
I (1)		I (1-3) I (2-3)	III (1-4) III (1-4)
I (1)		I (1) I (1)	II (1-3) II (1-3) II (2-3)
I (1-3)	III (1-3) III (1-3)	I (1) I (1-3)	
I (1-3)	II (1-4) II (1-3)	I (1-4) I (1-2)	I (2-5) I (1-4)
	II (1-3) II (1-3) I (1-3)	I (1-3)	
I (1-3)	I (1)		

Number of samples	51	56
Number of species/sample	21 (11–41)	29 (15–49)
Herb height (cm)	11 (4–30)	15 (3–30)
Herb cover (%)	64 (20–100)	86 (65–100)
Bryophyte height (mm)	12 (2–20)	30
Bryophyte cover (%)	41 (2–80)	49 (5–95)
Altitude (m)	364 (1–730)	310 (2–792)
Slope (°)	8 (0–30)	10 (0–35)
Soil pH	6.5 (5.8–7.2)	6.6

- a *Carex demissa*-*Juncus bulbosus/kochii* sub-community
- ai *Eleocharis quinqueflora* variant
- aii *Carex hostiana*-*Ctenidium molluscum* variant
- aiii *Schoenus nigricans* variant
- b *Briza media*-*Primula farinosa* sub-community
- bi *Cirsium palustre* variant
- bii *Molinia caerulea*-*Eriophorum latifolium* variant
- biii *Thymus praecox*-*Racomitrium lanuginosum* variant

36	9	20	26
22 (13–35)	41 (32–56)	34 (22–47)	32 (19–46)
<hr/>			
18 (10–35)			
76 (50–100)		80 (60–90)	76 (50–100)
10			
45 (5–80)		53 (30–80)	61 (20–90)
<hr/>			
80 (1–231)			
5 (0–17)		10 (3–20)	2 (0–10)
6.8			
<hr/>			

