M37
Cratoneuron commutatum-Festuca rubra spring

Synonymy
Tufaceous mounds Holdgate 1955*a p.p.*; *Cratoneuron commutatum-Saxifraga aizoides* nodum McVean & Ratcliffe 1962, Birks 1973; *Cratoneuron* springs Ferreira 1978; *Cratoneuron* drip-zones Ferreira 1978; *Cratoneuron commutatum* Community Birse 1980; *Cratoneuron filicinum* Community Birse 1980.

Constant species
Festuca rubra, *Bryum pseudotriquetrum*, *Cratoneuron commutatum*.

Physiognomy
Cratoneuron commutatum occurs frequently and with a measure of local abundance in a variety of calcareous mires, but in the *Cratoneuron commutatum-Festuca rubra* spring it is consistently dominant in large swelling masses, often forming prominent mounds or banks, of a golden-green colour grading to orange-brown. In some stands, which seem to preserve the same general floristic composition, *C. filicinum* accompanies or totally replaces it: the two species can show intergradations, and indeed both exhibit wide intraspecific variation (Bell & Lodge 1963, Smith 1978) but, by and large, *C. filicinum* is a smaller and somewhat stiffer plant and its stem leaves are plicate.

Other bryophytes can make a contribution to the mat, though typically it is a minor one. However, *Bryum pseudotriquetrum* is very common and occasionals include *Philonotis fontana* and the distinctly calcicolous *P. calcarea*, *Aneura pinguis*, *Pellia endiviifolia*, *Drepanocladus revolvens*, *Gymnostomum recurvirostrum*, *G. aeruginosum*, *Brachythecium rivulare* and *Dicranella palustris*. Very typically, there is some tufa deposition among the bryophyte shoots, which lends the mat a distinctive crunchy texture and allows it to build up into mounds.

The vascular element of the vegetation is typically species-poor and of low total cover with, in many stands, just a few scattered herbs. But there is considerable variation in this associated flora from place to place and, particularly where stands are developed over gently-sloping ground, a richer and more extensive herb layer can be found, such that the vegetation comes close to the *Cratoneuron-Carex* spring or to a Caricion davallianae flush. Often, however, the only species present are *Festuca rubra*, *Cardamine pratensis* and *Saxifraga aizoides*. The last can be quite conspicuous here, particularly when it has its yellow summer flowers, but it is generally present only in small amounts and is totally absent from springs of this kind throughout southern Scotland (e.g. Meek 1976, Ferreira 1978) and in Wales.

Occasional herbs include *Agrostis stolonifera*, *Deschampsia cespitosa*, *Equisetum palustre*, *Chrysosplenium oppositifolium*, *Poa trivialis*, *Carex panicea*, *C. nigra*, *C. dioica* and the rare *Epilobium alsinifolium* and *Equisetum variegatum*.

Habitat
This is a community of ground kept permanently moist by irrigation with base-rich, calcareous and generally oligotrophic waters. It is widespread but local throughout the cooler and wetter north-western uplands of Britain where springs and seepage lines occur in areas of lime-rich bedrocks. Trampling and grazing can have an adverse effect on the bryophyte carpet but in inaccessible positions the community is essentially permanent.

Like the *Philonoto-Saxifragetum*, this is a vegetation type dependent on the kind of sustained irrigation common in areas of higher rainfall. It is best developed in those parts of the country where there are more than 1600 mm precipitation annually (*Climatological Atlas* 1952), with in excess of 180 wet days yr^{-1} (Ratcliffe 1968), and here it can be found marking out springheads, seepage lines and drip-zones, where waters emerge along bedding-planes or at junctions with impervious substrates. Provided the ground is kept permanently sodden by the trickling or splashing waters, the community can occur even over vertical surfaces and bare rock, able to hang down in curtain-like masses by

virtue of the pleurocarpous habit of the *Cratoneuron* spp. and the binding of the dead shoots by tufa. In other cases, the vegetation has more of the character of a flush, with the dominant moss forming a carpet over more gently-sloping ground.

In all cases, however, the habitat is a base-rich and calcareous one, with pH values generally around 7 and, in stands sampled by McVean & Ratcliffe (1962), dissolved calcium levels between 23 and 39 mg l^{-1}. Throughout the uplands, then, the community is confined to lime-rich bedrocks or superficials, occurring over limestones, such as those of the Carboniferous in the Pennines (Holdgate 1955*a*, Pigott 1956*a*), and of Cambrian/Ordovician and Jurassic provenance on Skye (Birks 1973), and marking out limey partings in Ordovician/Silurian shales in the Moorfoot cleughs (Ferreira 1978). Stands can also be found on more basic igneous rocks, among the Borrowdale Volcanics, for example, and on calcareous metamorphic rocks, most notably on the Dalradian meta-sediments in the Scottish Highlands, where schists and epidiorites are especially important substrates and, more locally, among the Moine series (McVean & Ratcliffe 1962, Birse 1980). The community spans a wide altitudinal range, though it tends to be absent from the very highest ground where extremely heavy rain has surface-leached the weathering products of even calcareous rocks. The character of the soil mantle is varied: in many cases the profiles are primitive and fragmentary, amounting to little more than mineral detritus and rotting moss remains while, in other stands, there can be a more substantial base of silty, humus-rich mud beneath the mat. Commonly, too, there is the deposition of tufa among the moss shoots.

The calcareous character of this spring environment is reflected in the vegetation in the overwhelming dominance of the *Cratoneuron* spp., and the occasional occurrence of mosses such as *Philonotis calcarea* and *Gymnostomum recurvirostrum*, and the presence among the vascular component of *Saxifraga aizoides* and, much more occasionally, plants like *Carex dioica*, *C. pulicaris*, *Pinguicula vulgaris* and *Equisetum variegatum*. Where numbers of these are present together, they can give something of the richness and diversity of a Caricion davallianae flush, but the overwhelming dominance of the moss carpet typically precludes more than local expression of this. The freedom from grazing that occurrence on steeper slopes brings probably plays a large part in maintaining such dominance: in many base-rich flushes, trampling and nibbling of the herbage are important agents in maintaining an open, varied turf.

There is one further environmental feature that exerts some influence on the character of the vegetation. It is temperature, particularly the coolness of the air and flushing waters during the summer through much of the range of the community, which encourages the precipitation of tufa and imparts an Arctic-Alpine feel to the modest vascular flora. Thus, within the heart of the range of the *Cratoneuron-Festuca* spring, mean annual maximum temperatures rarely exceed 23 °C (Conolly & Dahl 1970) with annual accumulated temperatures usually below 500 day-degrees C (Page 1982). The Arctic-Alpine *S. aizoides* is the best reflection of such conditions here, although its range shows a striking gap in southern Scotland with outlying populations in the colder reaches of the Lake District and the north Pennines (Perring & Walters 1962). Other, less common, plants of this character are *Epilobium alsinifolium* and *Thalictrum alpinum*. Beyond the range of such species, springs dominated by *Cratoneuron* spp. can certainly be found and further sampling may reveal a distinct syntaxon of such vegetation. *C. filicinum* is certainly the more common of the two species at lower altitudes and it seems to be characteristic of somewhat more eutrophic irrigating waters (Oberdorfer 1977, Birse 1980). For the moment, however, it seems best to retain all the sampled variation within the same unit.

Zonation and succession

The *Cratoneuron-Festuca* spring is generally found as an integral part of very characteristic sequences of our more calcicolous upland communities, developed over ground that is progressively drier. Topographic and edaphic variation over exposures of lime-rich substrates can modify and fragment such zonations and grazing and trampling also often play a part in influencing the vegetation pattern.

Very commonly, the *Cratoneuron-Festuca* community marks out springs and seepage lines within tracts of calcicolous grasslands developed over drier rendzina soils or calcareous brown earths. Stands are typically small, frequently less than 1 m^2, though more extensive banks and curtains can sometimes be found, and where there is a repeated pattern of irrigation at points along a slope, whole series of springs can pick this out. In rockier situations, where seepage occurs directly from bedding planes in exposures, the stands are often well defined, with a sharp disjunction from the surrounds but, with more diffuse irrigation, particularly over gentle slopes that are open to grazing, much more gradual transitions can be seen.

The kinds of sward that surround the *Cratoneuron-Festuca* spring vary with the region and, within regions, with altitude. A common context is provided by the *Festuca-Agrostis-Thymus* grassland, the typical plagioclimax pasture of moist calcareous soils through much of the north-western uplands of Britain and a community which, on the flushed surrounds of springs, can grade to the *Cratoneuron-Festuca* vegetation through its *Carex* or *Saxifraga-Ditrichum* sub-communities. On the

limestones of the north Pennines, exactly parallel sequences can be seen between the springs and the *Sesleria-Galium* grassland which largely replaces the *Festuca-Agrostis-Thymus* grassland in this part of Britain, and which also has a *Carex* sub-community of moister soils. On the metamorphosed sugar-limestone of Upper Teesdale, the very distinctive *Carex capillaris-Kobresia* sub-community of the *Sesleria-Galium* grassland can be found in such patterns.

Small-sedge fens of the *Pinguiculo-Caricetum* also often occur on the strongly-flushed ground around or below *Cratoneuron-Festuca* springs and, where this community is interposed between the spring and the grassland, much more gradual transitions can be seen through the sequence of vegetation types with bryophytes such as *Cratoneuron commutatum*, *Bryum pseudotriquetrum* and *Aneura pinguis* running on into the flush as a broken carpet among the now much richer herb layer.

At higher altitudes, in the Scottish Highlands, for example, the *Cratoneuron-Festuca* spring can extend up to almost 1000 m and here it can be found among the more montane calcicolous communities like the *Festuca-Alchemilla-Silene* dwarf herb vegetation, an important context over the mica-schist slopes and banks of the Dalradian deposits. At these higher altitudes, too, there is a tendency for the *Pinguiculo-Caricetum* to be replaced by the *Cariceto-Saxifragetum* over the strongly-irrigated ground of open stony flushes below *Cratoneuron-Festuca* springs.

In more gradual transitions between the community and the surrounds, developed over gentler slopes, trampling by grazing stock or deer often plays an important part in maintaining the characteristically open conditions of the flushed soils. Typically, the *Cratoneuron-Festuca* spring itself is inaccessible to such treatment and heavy trampling is undoubtedly deleterious to the bryophyte mat. Such influences may indeed help convert the vegetation to a Caricion davallianae flush where springs occur on ground that is opened to pasturing, with an increase in the cover and diversity of smaller herbs able to exploit the lack of competition. The much richer *Cratoneuron-Carex* community described largely from Moor House in Cumbria (Eddy *et al.* 1969; see also Huntley 1979) may represent a stage in such a process.

In most circumstances, the *Cratoneuron-Festuca* spring appears to be a permanent community maintained by the edaphic and climatic conditions of the environment and, even where long ungrazed, it is unlikely that progression to any kind of woody vegetation is easy because of the impoverished character of the waters and soils. Where conditions are a little more eutrophic, however, lack of grazing could perhaps permit the spread of taller herbs. Over inaccessible dripping cliffs, the *Cratoneuron-Festuca* spring can sometimes be found with the *Alchemilla-Saxifraga* tall-herb community, in which *C. commutatum* and *B. pseudotriquetrum* form a patchy ground layer beneath tumbling masses of *S. aizoides* and a variety of calcicolous and mesophytic montane herbs.

Distribution

The community can be found over more lime-rich rocks throughout the north-western uplands of Britain, with its more Arctic-Alpine element best developed in the Scottish Highlands with outliers in the Lake District and Upper Teesdale. Springs dominated by *Cratoneuron* spp. also occur widely, though often very locally, in the British lowlands and further sampling of these is needed to provide a complete definition of this kind of vegetation.

Affinities

Although *C. commutatum* found early mention among general discussions of spring vegetation (e.g. Tansley 1911), this kind of community was not formally described until McVean & Ratcliffe's (1962) survey of stands in the Scottish Highlands. These form the core of the *Cratoneuron-Festuca* community as defined here, but such further sampling as has been undertaken shows that there is a gradation between the more Arctic-Alpine stands and *Cratoneuron* vegetation found at lower altitudes. Although more work is needed here, the general affinities of the vegetation are clear enough. They lie between the springs of the Cardamino-Montion, sharing such species as *Philonotis fontana*, *Cardamine pratensis*, *Deschampsia cespitosa* and *Chrysosplenium oppositifolium*, and the calcicolous small-sedge fens of the Caricion davallianae, where such plants as *Cratoneuron commutatum*, *Bryum pseudotriquetrum* and *Aneura pinguis* occur with a variety of basiphile herbs. Such vegetation is traditionally placed in the Cratoneurion to which *Cratoneuron* spp., *Philonotis calcarea* and *Saxifraga aizoides* are regarded as preferential (Ellenberg 1978).

Floristic table M37

Cratoneuron commutatum	V (4–10)
Festuca rubra	IV (1–6)
Bryum pseudotriquetrum	IV (1–5)
Cardamine pratensis	III (1–5)
Saxifraga aizoides	III (1–7)
Cratoneuron filicinum	II (2–9)
Agrostis stolonifera	II (2–5)
Philonotis fontana	II (1–6)
Deschampsia cespitosa	II (1–4)
Equisetum palustre	II (1–5)
Epilobium alsinifolium	II (2–5)
Chrysosplenium oppositifolium	II (2–7)
Aneura pinguis	II (1–3)
Carex panicea	II (2–4)
Carex nigra	II (1–6)
Poa trivialis	II (2–6)
Carex dioica	II (2–4)
Juncus articulatus	I (1–3)
Pinguicula vulgaris	I (1–4)
Poa pratensis	I (1–4)
Sagina procumbens	I (1–3)
Polygonum viviparum	I (1–5)
Taraxacum officinale agg.	I (1–3)
Drepanocladus revolvens	I (2–3)
Agrostis capillaris	I (2–4)
Agrostis canina	I (2)
Pellia endiviifolia	I (1–5)
Ctenidium molluscum	I (2–5)
Gymnostomum recurvirostrum	I (1–3)
Cerastium fontanum	I (1–2)
Brachythecium rivulare	I (1–5)
Festuca ovina	I (2–4)
Cochlearia officinalis	I (3–8)
Montia fontana	I (3–4)
Rumex acetosa	I (1–3)
Thalictrum alpinum	I (1–4)
Tussilago farfara	I (2–3)
Dicranella palustris	I (1–3)
Selaginella selaginoides	I (1–3)
Carex demissa	I (1–4)
Juncus bulbosus	I (1–3)
Carex flacca	I (2–3)
Carex lepidocarpa	I (2–7)
Alchemilla glabra	I (2)
Jungermannia exsertifolia	I (2)
Equisetum variegatum	I (2–3)
Carex pulicaris	I (2)
Caltha palustris	I (2–3)
Crepis paludosa	I (2–3)
Euphrasia officinalis agg.	I (1–3)
Hypericum pulchrum	I (1–2)
Blindia acuta	I (2–3)
Breutelia chrysocoma	I (1)
Gymnostomum aeruginosum	I (2–5)
Conocephalum conicum	I (1)
Holcus lanatus	I (1–4)
Triglochin palustris	I (2)
Eriophorum angustifolium	I (1–3)
Sagina nodosa	I (1–3)
Holcus mollis	I (2–4)
Number of samples	33

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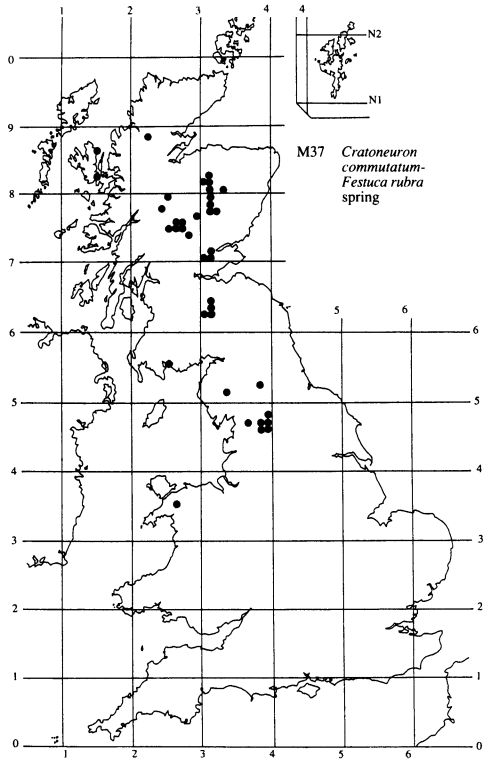

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