W20
Salix lapponum-Luzula sylvatica scrub

Synonymy
Willow scrub Poore & McVean 1957 *p.p.*; *Salix lapponum-Luzula sylvatica* nodum McVean & Ratcliffe 1962; Montane willow scrub association McVean 1964; *Salix lapponum-Vaccinium myrtillus* nodum Huntley 1979.

Constant species
Salix lapponum, *Deschampsia cespitosa*, *D. flexuosa*, *Luzula sylvatica*, *Vaccinium myrtillus*, *Dicranum scoparium*, *Hylocomium splendens*, *Rhytidiadelphus loreus*.

Rare species
Carex atrata, *Polystichum lonchitis*, *Salix arbuscula*, *S. lanata*, *S. lapponum*, *S. myrsinites*, *S. reticulata*.

Physiognomy
Isolated bushes of Arctic-Alpine and Arctic-Subarctic willows figure occasionally in higher-altitude stands of the moderately calcicolous kinds of ungrazed vegetation included in the *Luzula-Vaccinium* and *Luzula-Geum* communities but in some situations these willows are so abundant as to constitute a low bushy canopy to this *Salix lapponum-Luzula sylvatica* scrub with associated changes in the accompanying flora. Of the various willows represented here, *Salix lapponum* is the commonest and most widely distributed and usually it dominates, its much-branched bushes forming a patchy cover up to a metre or so high. But it can be accompanied or sometimes replaced by the generally smaller *S. myrsinites* or by *S. lanata*, especially prominent in the Clova-Caenlochan area (e.g. Huntley 1979), or *S. arbuscula*, particularly distinctive around Breadalbane (McVean & Ratcliffe 1962, Ratcliffe 1977). In some sites, too, drawn-up shoots of the normally diminutive *S. reticulata* make a contribution to the cover and very occasionally the canopy is further enriched by bushes of more widely distributed willows like *S. cinerea* and *S. phylicifolia*. Hybrid willows are sometimes found but sexual reproduction even within the rarer species may be very infrequent: in many areas, the number of bushes is small and the sexes often widely separated (McVean 1964*a*).

There are usually some sub-shrubs growing among the willows. The commonest of these is *Vaccinium myrtillus*, which can be co-dominant, but *V. vitis-idaea*, *Empetrum nigrum* ssp. *hermaphroditum* and *Calluna vulgaris* all occur frequently and *V. uliginosum* occasionally, though generally their cover is low. Often more prominent is a strong contingent of grazing-sensitive herbs, the luxuriant growth of which among the shrubby canopy gives this kind of scrub a very distinctive look. *Luzula sylvatica* is the most frequent member of this group, its tussocky mats sometimes forming an extensive cover and hanging down from ledges in festoons, but other species are *Alchemilla glabra*, *Geum rivale*, *Rumex acetosa*, *Angelica sylvestris*, *Galium boreale* and the Arctic-Alpine *Rhodiola rosea*, *Oxyria digyna* and *Saussurea alpina*. Somewhat less frequently, there are records for *Solidago virgaurea*, *Succisa pratensis*, *Filipendula ulmaria*, *Valeriana officinalis*, *Coeloglossum viride* and Hieracia (not recorded to the species, but presumably mostly of the Alpina, Subalpina and Cerinthoidea sections: see Raven & Walters 1956); and occasionally there is some *Dryopteris dilatata* or *Thelypteris phegopteris* with *Polystichum lonchitis* and *Blechnum spicant* occurring rarely.

Among these is an equally rich and diverse assemblage of herbs of somewhat smaller stature. Continuing the Arctic-Alpine contribution are *Alchemilla alpina*, *Thalictrum alpinum*, *Polygonum viviparum* (all very frequent), *Saxifraga oppositifolia* (occasional) and *S. stellaris*, *S. aizoides*, *Epilobium anagallidifolium* (all scarce). But also very common are *Galium saxatile*, *Viola riviniana*, *Campanula rotundifolia*, *Oxalis acetosella* with, somewhat less frequently, *Huperzia selago*, *Ranunculus acris*, *Philonotis fontana*, *Selaginella selaginoides*, and, very occasionally, *Caltha palustris*, *Euphrasia officinalis* agg., *Rhinanthus minor*, *Anemone nemorosa* and *Thymus praecox*.

Then, there is usually some contribution from grasses,

typically growing as discrete tussocks. *Deschampsia cespitosa* (sometimes viviparous) and *D. flexuosa* are the commonest species and generally the most abundant, but *Festuca ovina* (and *F. vivipara* when recorded separately), *Agrostis canina*, *A. capillaris*, *Anthoxanthum odoratum* all occur quite frequently and *Festuca rubra* and *Nardus stricta* more occasionally. *Carex bigelowii*, *C. binervis* and, more rarely, *C. flacca* and the Arctic-Alpine *C. atrata* have also been recorded here. The total vascular flora of this kind of vegetation is thus very large and individual stands are characteristically rich, though the contribution from the various components and species is typically diverse and, in any single locality, the frequencies of the occasional associates can show considerable variation.

The same feature is true of the bryophyte element. Very common throughout the community and often forming a thick, luxuriant carpet are *Hylocomium splendens*, *Rhytidiadelphus loreus*, *Dicranum scoparium*, *D. majus*, *Mnium hornum*, *Ptilidium ciliare*, *Pleurozium schreberi*, *Thuidium tamariscinum* and *Sphagnum subnitens*. Rather less frequent are *Rhytidiadelphus triquetrus*, *R. squarrosus*, *Polytrichum alpinum*, *Rhizomnium punctatus*, *Plagiomnium undulatum*, *Plagiothecium undulatum*, *Hypnum cupressiforme* and a variety of Sphagna, *S. girgensohnii*, *S. russowii*, *S. capillifolium*, *S. palustre*, *S. recurvum*, *S. teres* and *S. squarrosum*. Other scarce bryophytes include *Hypnum callichroum*, *Ptilium crista-castrensis*, *Drepanocladus revolvens*, *D. uncinatus*, *Ctenidium molluscum*, *Fissidens adianthoides* and *Cratoneuron commutatum*.

Lichens are generally sparse but *Peltigera canina* may be conspicuous and there can be some *Cladonia squamosa* or *C. pyxidata*.

Habitat

The *Salix-Luzula* scrub is a community of ungrazed, high-altitude rocky slopes and ledges with wet, mesotrophic and base-rich soils. It probably represents the sub-alpine climax vegetation in such situations, though herbivore predation has reduced it to the status of a relic community of generally small, isolated stands, a fragmentation which affects the composition and structure of the community.

The *Salix-Luzula* scrub is the most high-level kind of tree- or shrub-dominated vegetation in Britain, the altitudinal range of available samples being from 630 m to over 900 m: it overlaps a little with the *Juniperus-Oxalis* woodland where *Juniperus communis* ssp. *communis* and *Betula pubescens* ssp. *carpatica* can dominate on drier, more acidic soils but the mean altitude of stands here is over 300 m higher. Apart from some fragmentary stands in the Moffat Hills in Dumfries (Ratcliffe 1959*b*, 1977), the community is confined to the Scottish Highlands where there is a harsh montane climate with long, bitter winters and short, cool summers. The annual accumulated temperature lies within the range 277–556 °C (500–1000°F) (Gregory 1954) and the mean annual maximum temperature is less than 21 °C (Conolly & Dahl 1970), conditions which are strongly reflected in the vegetation by the large contingent of Arctic-Alpine species, not least the willows themselves. Annual precipitation is generally more than 1600 mm (*Climatological Atlas* 1952), with at least 180 wet days yr^{-1} (Ratcliffe 1968) but, at these altitudes, much of this falls as snow in the winter months and, with the lateness of spring, this tends to be long on the ground.

Late snow-lie is especially marked in the east-central and southern Highlands where the *Salix-Luzula* scrub has its centre of distribution but, throughout its range, there is a tendency for stands to occupy sites with a north to east aspect which would afford some protection against early melt. McVean & Ratcliffe (1962) suggested that a snow cover might be important in localising the occurrence of the willows by giving some shelter from air frosts, very frequent and occurring into late spring at these altitudes. Whether this is always the case has been questioned (Huntley 1979), though comparable communities in Scandinavia are clearly associated with long snow-lie (e.g. Nordhagen 1928, 1943, Dahl 1956).

Within this climatic zone, the *Salix-Luzula* scrub is typically found on soils with a degree of base-, and probably nutrient-, enrichment. It is distinctly associated with more calcareous rocks, notably among the Dalradian meta-sediments of the central and southern Highlands, where it occurs on banks and ledges in limestones, mica-schists and epidiorite intrusions in Breadalbane and the Clova-Caenlochan hills (Ratcliffe 1977, Huntley 1979), and, more locally, on the Moine Assemblage, as on Creag Meagaidh in Inverness and on Ben Hope in Sutherland (Ratcliffe 1977). In the Moffat Hills, fragmentary stands are found on calcitic crush-zones (Ratcliffe 1959*b*). However, the soils are not the kind of alpine rendzinas typical of the *Dryas-Silene* community. Characteristically, seepage of ground water is strong and the profiles are permanently wet and usually unstructured accumulations of silt and rock fragments, often unstable and, on the steepest slopes, retained only by the mat of vegetation rooted into the rocks. Very few analytical data are available from these soils but McVean & Ratcliffe (1962) recorded pHs of 5.7 and 6.9 under two stands with similar amounts of calcium as in the *Dryas-Silene* community and the more calcicolous kinds of *Festuca-Agrostis-Thymus* grassland. Litter incorporation and turnover of such nutrients as there are in the system are probably quite rapid with the abundance of *Luzula sylvatica* in particular tending to favour the development of moder humus.

The floristic response to these edaphic conditions is

quite varied. A strictly calcicolous element in the vegetation is not well defined, though, among the willows themselves, *S. lanata*, *S. myrsinites*, *S. arbuscula* and *S. reticulata* are fairly exacting species (McVean & Ratcliffe 1962) and some plants may be largely or totally excluded by competition from the tall herbage (e.g. *Saxifraga oppositifolia*, *Thymus praecox*, *Carex flacca*, *C. pulicaris*) or by the wetness of the soils (e.g. *Polystichum lonchitis*). Much more obvious is a group of species indicative of mesotrophic conditions, often associated in the uplands with base-enrichment: among these would figure *S. lapponum*, most of the tall herbs, *Viola riviniana* and bryophytes like *Thuidium tamariscinum* and *Plagiomnium undulatum*. But calcifuges are quite strongly represented here with *Vaccinium myrtillus* and other sub-shrubs and a number of more exacting bryophytes: this may be a measure of soil heterogeneity across larger ledges or a reflection of some vertical differentiation in the profile with a patchy surface mat of litter, humus and bryophytes insulated somewhat from seepage through the mineral layer beneath.

Even where these climatic and edaphic requirements are met, the *Salix-Luzula* scrub is found only over very rocky slopes and on ledges whose inaccessibility affords protection from grazing and browsing by deer and sheep (and, in some areas in the past, cattle, as at Caenlochan: Huntley 1979). One very characteristic type of site which combines such features is the complex of fairly steep slopes below series of low cliffs associated with sequential waterfalls, where the severe topography prevents access to herbivores from above and below. The community is not, however, invariably present on all such suitable sites, being often replaced by various kinds of *Luzula-Geum* or *Luzula-Vaccinium* communities on identical soils. Variation in exposure and snow-lie may play some part in such differentiation but, often, the absence of willows may be simply a question of loss through death of existing bushes and failure to re-invade. Individuals of some of these species may not be long-lived, despite their sometimes gnarled and venerable appearance (Meikle 1984) and, with the progressive isolation of populations with centuries of pastoral exploitation of the uplands and often wide separation of the sexes (Poore & McVean 1957), continued colonisation may be very difficult. Where the community does persist, the physical configuration of the rock exposures and ledges affects the physiognomy and floristics of the vegetation by the simple limitation of space and the presentation of surfaces of different shape and slope.

Zonation and succession

Most commonly, zonations from the *Salix-Luzula* scrub to other vegetation types are a reflection of variations in grazing pressure though, since these typically relate to differences in topography, edaphic factors sometimes play a part.

Usually, the community occurs as small stands isolated on rocky knolls and ledges within a montane landscape largely transformed by grazing to various kinds of close-cropped grassy or herb-dominated swards. In areas where calcareous rocks and soils are more common, as over the Dalradian schists and limestones of Breadalbane and in the Clova-Caenlochan district, the *Salix-Luzula* scrub overlaps altitudinally with more high-level stands of the *Festuca-Agrostis-Thymus* grassland and the *Festuca-Agrostis-Alchemilla* grass-heath. More flushed types of these two communities show strong floristic affinities with the *Salix-Luzula* scrub and have probably been derived from it by elimination of willows and tall herbs and a favouring of grasses and grazing-resistant dicotyledons. At higher altitudes, the community can also be found in association with the *Festuca-Alchemilla-Silene* dwarf-herb community in which grazing-tolerant Arctic-Alpines are well represented and this kind of vegetation, too, may be a derivative of *Salix-Luzula* scrub, though it is characteristic of more exposed situations where solifluction and cryoturbation are important, so this transition may be partly an edaphic one. Floristically and environmentally, the *Dryas-Silene* community can be seen as intermediate between the *Festuca-Alchemilla-Silene* community and the *Salix-Luzula* scrub. Typically, it is much less heavily grazed than the former, though often in more unstable situations than the latter and it can occasionally have some of the larger Arctic-Alpine willows. Good transitions from the *Dryas-Silene* community to the *Salix-Luzula* scrub can be seen on Meall na Samhna, Carn Gorm and Beinn Dearg (Ratcliffe 1977), the willows increasing their cover in the latter vegetation and shading out many species of the former. Where calcareous rocks and soils form a much more local intrusion into landcapes dominated by acidic substrates, as among the Moinian and Lewisian rocks of the Cairngorms and the north-west Highlands, floristic transitions are usually much sharper: here ledges with the *Salix-Luzula* scrub may be surrounded by a small zone of more calcicolous grassland on flushed soils but often there is a fairly quick zonation to calcifuge grasslands and heaths on base-poor brown earths, gleys and peaty soils.

In both these kinds of situations, the community typically occupies only some of the available ledges, others supporting very similar *Luzula-Geum* vegetation or, where flushing is with somewhat less base-rich waters, the *Luzula-Vaccinium* community. How far the willows could spread into these other vegetation types or into flushed, calcicolous swards, if grazing were to be reduced, is unknown. Reconstitution of the *Salix-Luzula* scrub would probably be very difficult, though enclosure of the surrounds of some more vigorous and

mixed-sex willow populations would be an instructive exercise. On the Durness Limestone above Inchnadamph, Poore & McVean (1957) sampled a low-altitude scrub (210–274 m) where *Salix myrsinites* seemed to have re-invaded *Festuca-Agrostis-Thymus* grassland and such expansion might be possible at higher levels.

By and large, however, the *Salix-Luzula* scrub persists now as remnants isolated well above any other kind of woody vegetation. It seems reasonable to suppose, comparing the Scottish situation with Scandinavia, where similar vegetation is widespread, that the community was at one time much more common, replacing scrubby hazel-, rowan- and birch-dominated *Fraxinus-Sorbus-Mercurialis* woodland at high altitudes on wet, calcareous soils. Nowhere, now, do such zonations persist intact.

Distribution

The community is widespread but local through the southern and central Highlands of Scotland, being especially well-developed in Breadalbane and around Clova-Caenlochan, with more isolated stands in the north-west Highlands and, far to the south, in the Moffat Hills. *Salix lapponum* survives at high altitudes on Helvellyn in the Lake District, though it occurs there on rather dry rocks without the luxuriant assemblage typical of the *Salix-Luzula* community.

Affinities

The definition of the *Salix-Luzula* scrub is based on the data of McVean & Ratcliffe (1962) and Huntley (1979) with no further sampling. The nearest equivalents to the community in Europe are the various kinds of sub-alpine willow scrub described from Scandinavia by Nordhagen (1928, 1943) and Dahl (1956), particularly the *Salicetum geraniosum alpicolum* from Sikilsdalen (Nordhagen 1943) and the *Rumiceto-Salicetum lapponae* from the Rondane area (Dahl 1956). However, two features are notable in comparing these vegetation types with our own montane willow scrub: first, the former are generally much richer in tall herbs, having a field layer more like that of our wetter *Fraxinus-Sorbus-Mercurialis* woodland (*Crepis* sub-community); and, second, in Scandinavia, the Arctic-Alpine willows also extend into mire vegetation like that of the *Carex saxatilis* and *Carex rostrata-Sphagnum warnstorfii* mires. The *Salix-Luzula* scrub clearly belongs among the sub-alpine and alpine tall-herb communities of the Betulo-Adenostyletea, in which Ellenberg (1978) has distinguished a Salicion arbusculae with prominent dwarf willows.

Floristic table W20

Salix lapponum	V (1–9)	*Galium saxatile*	III (1–3)
Salix lanata	II (4–7)	*Viola riviniana*	III (1–3)
Salix myrsinites	II (4–8)	*Pleurozium schreberi*	III (1–4)
Salix reticulata	II (1–5)	*Sphagnum subnitens*	III (1–8)
Salix arbuscula	I (6)	*Thuidium tamariscinum*	III (1–5)
Salix phylicifolia	I (5)	*Vaccinium vitis-idaea*	III (2–3)
Salix cinerea	I (2–3)	*Festuca ovina*	III (3–4)
Vaccinium myrtillus	V (1–7)	*Angelica sylvestris*	III (1–5)
Hylocomium splendens	V (2–8)	*Thalictrum alpinum*	III (2–3)
Rhytidiadelphus loreus	V (1–7)	*Polygonum viviparum*	III (1–3)
Deschampsia flexuosa	IV (2–5)	*Agrostis canina*	II (2–3)
Luzula sylvatica	IV (1–8)	*Campanula rotundifolia*	II (1–3)
Deschampsia cespitosa	IV (2–5)	*Galium boreale*	II (1–3)
Dicranum scoparium	IV (1–5)	*Rhizomnium punctatum*	II (1–5)
Alchemilla alpina	III (2–5)	*Rhytidiadelphus triquetrus*	II (1–5)
Alchemilla glabra	III (1–6)	*Sphagnum girgensohnii*	II (2–6)
Geum rivale	III (1–6)	*Plagiochila asplenoides*	II (1–2)
Rumex acetosa	III (1–4)	*Dryopteris dilatata*	II (1–3)
Rhodiola rosea	III (1–4)	*Oxalis acetosella*	II (1–3)
Dicranum majus	III (1–6)	*Plagiothecium undulatum*	II (2–3)
Mnium hornum	III (1–3)	*Polytrichum alpinum*	II (1–2)
Ptilidium ciliare	III (1–3)	*Selaginella selaginoides*	II (2)
Empetrum nigrum hermaphroditum	III (2–5)	*Rhytidiadelphus squarrosus*	II (1–2)
		Sphagnum palustre	II (1–3)

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Agrostis capillaris	II (2–3)
Carex bigelowii	II (1–2)
Oxyria digyna	II (1–3)
Saussurea alpina	II (1–5)
Plagiomnium undulatum	II (2–3)
Calluna vulgaris	II (2–3)
Anthoxanthum odoratum	II (2–5)
Solidago virgaurea	II (1–2)
Saxifraga oppositifolia	II (1–3)
Hypnum cupressiforme	II (2–4)
Huperzia selago	II (1–3)
Diplophyllum albicans	II (2)
Lophocolea bidentata s.l.	I (1–3)
Festuca rubra	I (2–3)
Epilobium anagallidifolium	I (1–2)
Sphagnum teres	I (1–3)
Chiloscyphus polyanthos	I (1–2)
Vaccinium uliginosum	I (1–6)
Hypnum callichroum	I (1–2)
Ranunculus acris	I (2–3)
Ptilium crista-castrensis	I (2–4)
Succisa pratensis	I (1–4)
Philonotis fontana	I (1–3)
Peltigera canina	I (1–4)
Carex binervis	I (1–4)
Filipendula ulmaria	I (2–4)
Racomitrium lanuginosum	I (2–4)
Saxifraga aizoides	I (2–3)
Drepanocladus revolvens	I (2)
Plagiothecium denticulatum	I (2)
Hieracium sp.	I (1–2)
Cladonia squamosa	I (2–3)
Thelypteris phegopteris	I (2)
Caltha palustris	I (3–4)
Saxifraga stellaris	I (1)
Calliergon cuspidatum	I (2)
Dicranum bonjeanii	I (1–2)
Drepanocladus uncinatus	I (2–3)
Sphagnum recurvum	I (1–2)
Sphagnum squarrosum	I (2–4)
Atrichum undulatum	I (1–2)
Sphagnum capillifolium	I (1–2)
Sphagnum russowii	I (1)
Thymus praecox	I (2–3)
Nardus stricta	I (3)
Euphrasia officinalis agg.	I (2–3)
Rhinanthus minor	I (1–2)
Valeriana officinalis	I (3–4)
Aulacomnium palustre	I (2–3)
Coeloglossum viride	I (1)
Saxifraga hypnoides	I (2–3)
Carex atrata	I (1–2)
Fissidens adianthoides	I (2)
Ctenidium molluscum	I (3)
Carex flacca	I (2)
Scapania undulata	I (2–3)
Cratoneuron commutatum	I (2–3)
Anemone nemorosa	I (2–4)
Barbilophozia barbata	I (2–3)
Luzula multiflora	I (2)
Number of samples	19
Number of species/sample	40 (29–58)
Vegetation height (cm)	58 (15–90)
Vegetation cover (%)	94 (70–100)
Altitude (m)	787 (630–914)
Slope (°)	40 (10–90)

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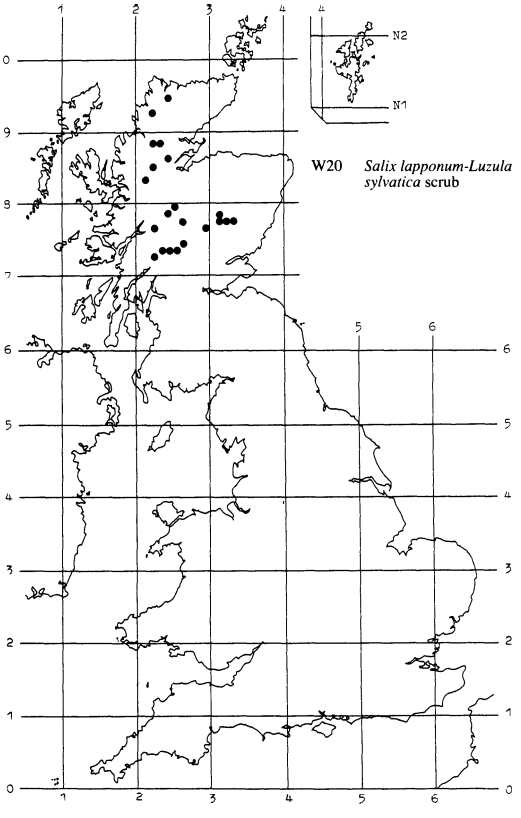

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