*British & Irish Botany* 4(3): 314-346, 2022

# The *Deschampsia cespitosa* (Poaceae) complex in Great Britain and Ireland

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This pdf constitutes the Version of Record published on 9th September 2022

## Abstract

The *Deschampsia cespitosa* complex in Great Britain and Ireland is shown to consist of three distinct species, one represented by three variants:
(1) *D. parviflora* (Thuill.) P. de Beauvois, a shade tolerant diploid species with spikelets less than 3.5 mm, of heavy clay or flushed soils in ancient woodland, principally from East Inverness-shire and central Scotland southwards;
(2) *D. alpina* (L.) Roemer and Schultes, a small, tetraploid, viviparous species, with hooded leaf-tips and brittle plantlets with appressed glumes and lemmas, of wet, open habitats at high altitudes in the Scottish Highlands and (rarely) in Ireland;
(3) *D. cespitosa* (L.) P. de Beauvois, represented by three variants,
(a) a seed-bearing diploid found primarily in peripheral coastal areas and islands in northern and western Scotland and on mountains in the central and northern Scottish Highlands and Teesdale,
(b) a seed-bearing tetraploid which is the common cytotype of the species in unshaded and many woodland habitats from central Scotland southwards,
(c) a viviparous tetraploid, which is a form of the seed-bearing tetraploid, found in the south-west Scottish Highlands, English Lake District and Snowdonia and is probably unique to Britain.

Suspected viviparous triploid hybrids were found between diploid *D. cespitosa* and both *D. alpina* and tetraploid *D. cespitosa*.

**Key Words:** taxonomy; chromosome numbers; ancient woodland; vivipary in grasses; phytogeography

## Introduction

There have been several attempts to produce a comprehensive taxonomic treatment of the *Deschampsia cespitosa* (L.) Beauv. complex in Great Britain and Ireland (Wycherley 1953, 1954; Hubbard 1954, 1984; Hedberg 1958; Rothera & Davey 1986; Cope & Gray, 2009). However, none has been wholly satisfactory. Although the extreme variants of the complex are very distinct, it has proved difficult to define discrete taxa. One particular problem has been the difficulty in identifying the viviparous (strictly pseudoviviparous) plants (Elmqvist & Cox, 1996; Hedberg, 1986).

The taxonomic confusion is reflected in the very wide definition of *D. cespitosa,* covering plants of very variable morphology from a very wide range of habitats, even within Great Britain and Ireland. These habitats range from shady, sheltered woodland through wet, grassy heathland to exposed grasslands from sea level to 1300m with soil pH values varying from acidic to highly alkaline (Davy, 1980; Grime *et al.*, 1988). The only consistent feature of these habitats is a requirement for moist to wet soil. Such morphological and habitat variation, taken together with reports of the presence of different ploidy levels within the species (Clarke, 1980), suggested that more than one breeding unit existed in *D. cespitosa.* It was considered that careful morphological study of plants of different ploidy level might allow the definition of more meaningful taxa with narrower morphological and ecological limits.

## Material and methods

In 1967, observations made on viviparous Scottish mountain *D. cespitosa* agg. plants maintained in cultivation showed that collections from the south-west Highlands were quite distinct from those from the north-west Highlands (McAllister, 1973; 1994). Further collections of both viviparous plants and associated non-viviparous plants were therefore made throughout Scotland and the upland areas of northern England, Wales and Ireland (Fig. 1 & Appendix I). Collections were made from 132 separate locations.

**Figure 1. Locations of collections of *Deschampsia cespitosa* agg. in Great Britain & Isle of Man. Two locations in Ireland (Brandon & Mangerton Mts.) are not mapped**

Where possible herbarium specimens of the wild plants were also taken and a few plantlets or tillers of each clone were collected and grown. The morphology of these plants was examined, herbarium specimens made and root tips taken for chromosome counting. Living material was also obtained from outside Great Britain and Ireland (Continental Europe, Turkey, Norway, Iceland, Greenland, Quebec, Spitsbergen and Siberia) and herbarium specimens examined from throughout the world.

## Cytological methods

Rothera and Davy (1986) found considerable difficulties in obtaining reliable counts of chromosomes within the *D. cespitosa* complex. Many aneuploid numbers have been reported by these and previous workers. To overcome this problem a modification of Dyer's lacto-propionic orcein method was used (Dyer, 1963). The root tips were squashed in an undiluted saturated solution of orcein in 1 : 1 lactic : propionic acid and the preparations examined using phase contrast microscopy. More recently counts have been obtained from squashes mounted in a 3 : 2 lactic-propioinic acid mixture without orcein.

Rapidly growing root tips were pretreated with a saturated solution of mono-bromo-naphthalein to accumulate metaphase plates through the inhibition of spindle formation. The root tips were incubated in vials either at room temperature (4h) or at 4°C (12-18h). Length of time was critical, especially at room temperature. Short treatment times resulted in elongated chromosomes which were intertwined, making counting difficult. Excessively long treatment times allowed chromosomes to separate into their constituent chromatids, or centromeres and secondary constrictions became stretched, resulting in elevated counts. When this occurred further preparations were made.

After pretreatment the root tips were fixed in 1 : 3 methanoic (acetic) acid : ethanol (98% industrial) for at least 24 hours in a refrigerator before hydrolysis in 1M hydrochloric acid at 60°C for 5 minutes and transfer to 70% ethanol for storage. Before squashing, root tips were placed in a drop of 70% ethanol on a microscope slide and, under x70 magnification, the root cap and firm outer layers of the root tip (periblem) were removed and the softer, inner part (plerome - incipient vascular strand) transferred to a drop of the mountant. These softer tissues were then macerated with needles and tapped under a coverslip to separate the cells. The preparation was then squashed and examined for cells containing well-separated chromosomes using phase-contrast, oil-immersion microscopy with anisole (methyl-phenyl ether) as the immersion liquid.

## Viviparous variants

Examination of all the viviparous plants grown under cultivation showed that there were two groups, loosely based on geographic location, southern and northern.

### *Southern viviparous*

This viviparous variant appears to be confined to Great Britain as no specimens seen from outside Britain were similar. These viviparous plants were tetraploid (2n=52), or occasionally triploid (2n=39), and seed-bearing *D. cespitosa* collected nearby was always tetraploid. When these plants were propagated from plantlets it took two years to produce a mature tussock with panicles.

This variant is more or less confined to the south-west Highlands of Scotland in an area bounded by Ben Cruachan in the West, Glen Etive in the North, Arrochar in the South and Ben More (Crianlarich) in the East, although it is also found on Scafell Pike in the Lake District, and in Snowdonia in North Wales. The records for the Scottish central lowlands given in McAllister (1994) are errors.

This variant has large vigorous tussocks resembling *Deschampsia cespitosa sensu stricto*, indeed, without panicles they are indistinguishable from *D. cespitosa.* Some individuals produce totally viviparous panicles with only proliferous spikelets while others produce mixed panicles of proliferous and non-proliferous spikelets which yield viable seed, at least in cultivation. Plantlets require two years growth to be mature enough to produce panicles. The height of the plants when grown in cultivation, both vegetatively and when bearing panicles, was always comparable with *D. cespitosa s.s*. grown under similar conditions - usually 1-1.5 m. The viviparous panicles had the same form as those of *D. cespitosa* until the development of the plantlets, which, being heavier than flowers or seeds, caused the panicle branches to droop. The plantlets were always firmly attached and it was only rarely that detached plantlets were found, either in the wild or in cultivation. Field observations indicate that panicles usually fall to the ground intact and the plantlets either produce roots and become established *in situ*, or are washed or blown for short distances before rooting.

The altitudinal range of this viviparous variant is from 600 m to 900 m, descending to 400 m on stream sides. Its habitat is either dense, wet grassland dominated by seminiferous (seed-bearing) *D. cespitosa s.s*. and this viviparous variant, or well-vegetated wet ledges. It is almost always found in association with non-viviparous *D. cespitosa* and always in the wettest parts of the habitat. Presumably constant surface moisture is needed for plantlet establishment.

*Northern viviparous*

Elsewhere in Great Britain and Ireland (i.e. the central and north-west Scottish Highlands and SW Ireland) and in arctic Russia, Scandinavia, Iceland, Greenland, Canada and probably Germany, viviparous *Deschampsia* is a different taxon.

These plants are small, rarely more than 0.6 m, the tillers are divergent at their bases and form a rather open tussock; dense tussocks like those of *D. cespitosa s.s*. are never formed. Often a plant in the wild may consist of only a few tillers, several of which may be producing panicles. This is very different from *D. cespitosa s.s*. and the southern viviparous variant in which only large tussocks appear capable of producing panicles. This northern viviparous variant has distinctly keeled and often folded leaves, small, triangular panicles and ovate spikelets, and could perhaps be mistaken for a viviparous *D. flexuosa*. It appears to be totally viviparous in Britain, Iceland and Scandinavia as no non-proliferous spikelets or seeds have been observed. The panicle shape is usually different from that of *D. cespitosa*, often being distinctly triangular and somewhat secund, usually with deflexed panicle branches which are weak and thus tend to hang. The attachment of the plantlets to the panicle is very brittle, even from the time of emergence from the sheath. When propagated from plantlets only one year is required to produce a mature tussock bearing panicles. The differences between the two viviparous types are summarised in the key below, but the most reliable single distinguishing character is in the nature of the leaf apex: tapering in the southern viviparous type, and distinctly and abruptly hooded, almost like the leaf tip of a *Poa*, in the northern variant.

The habitat of this smaller, northern variant is always very open communities on wet gravelly or peaty soils high in the mountains, rarely below 900 m but descending to lower levels in the Hebrides. It is often found in areas with late snow lie, presumably because its vivipary enables it to produce propagules in a short cold growing season. Associated species are often only bryophytes, but include such vascular species as *Huperzia selago, Micranthes (Saxifraga) stellaris, Oxyria digyna* and *Cerastium cerastioides* (McAllister, 1994)

While these viviparous plants are tetraploid (2n=52), associated seminiferous *D. cespitosa* is diploid (2n=26).

Within the area of the northern viviparous variant in the Scottish Highlands occasional viviparous plants are found which bear some resemblance to the southern viviparous variant. Such plants from South Uist in the Outer Hebrides, Glen Coe, the Ben Alder area and Mull are triploids and are presumably hybrids between the tetraploid northern viviparous variant and the diploid northern seminiferous *D. cespitosa.* However, these greatly resemble the northern viviparous variant, differing mainly in their smaller, more numerous spikelets and less triangular, more crowded panicles. They have presumably resulted from viable pollen from tetraploid viviparous plants fertilising diploid *D. cespitosa.*

*Areas of geographical overlap*

Both viviparous variants have been found on two mountains, Ben Ime (Grid Ref NN260076 - NN258083) and Ben Cruachan (Grid Ref. NN072302 & NN072306). On Ben Ime the southern viviparous variant is common in the grassland from about 560 m to the summit (*c.*1000 m) whereas the northern type is confined to very wet, largely unvegetated, peaty flushes around 900 m on the southern slopes. On Ben Cruachan the southern variant is again common in the grassland over a wide altitudinal range (350-1100 m) while the northern variant occurs only in Coire Caorach in a late snow patch area with bryophyte dominated vegetation and a northerly aspect at about 1050 m (Fig.2).

*Taxonomic status of the viviparous variants*

Before attempting to devise a taxonomic treatment for the two viviparous variants, the variation within each must be examined and some understanding reached of their relationship to seminiferous *Deschampsia*.

The southern viviparous variant is extremely variable. Several distinct clones can usually be recognised on each mountain, often growing mixed together but with many individual tussocks being referable to each clone. The majority of viviparous plants appear to be totally viviparous, at least in the wild, but partially viviparous plants occur occasionally in the wild and some plants which are wholly viviparous in the wild produce mixed panicles in cultivation. Partially viviparous or non-viviparous panicles are similar to those of the neighbouring non-viviparous *D. cespitosa,* suggesting that each viviparous clone may have arisen on the mountain on which it is now found, probably from non-viviparous ancestors. This means that there is probably no common viviparous ancestors to the viviparous plants on different mountains.

Some clues as to how the vivipary may have evolved can be gathered from observations on plants in cultivation. Seed-bearing diploids are well-known to occasionally produce viviparous panicles late in the growing season when day lengths are marginal for induction of flowering (Wycherley, 1954, Kawano, 1966). However, in twenty years of observing the species in the wild and in cultivation, this phenomenon has been observed only once, in a single panicle in Grass Woods, nr. Grassington, (Grid ref. SD984654) Wharfedale, Yorkshire in 1977.

Tetraploids, on the other hand, seem to produce viviparous panicles much more readily in cultivation. The only site where plants viviparous in the wild became totally non-viviparous in cultivation was Wet Sleddale, near Shap, Cumbria, (Grid ref. NY552152) where several viviparous plants were seen on the banks of the reservoir where the water had been drawn down. These plants had clearly been under water for some time in the winter and spring and so had experienced a shortened growing season. In cultivation, seed-bearing tetraploids collected on Corserine (Grid ref. NX500870) in Kirkcudbrightshire, Scotland produced a large number of normal, wholly seed-bearing panicles, but four of the six plants in cultivation also produced 2-3 shorter, totally viviparous panicles later in the season. A tetraploid from Cwm Idwal (Grid ref. SH6458) in north Wales which bore only seed-bearing panicles in the wild has borne only panicles with both viviparous and seed-bearing spikelets in cultivation. Tetraploids which were totally viviparous when gathered on Scafell Pike (Grid ref. NY221081) bore a mixture of totally viviparous and totally seed-bearing panicles in cultivation.

Viviparous tetraploids of the southern variant may be no more than selections out of the surrounding seed-bearing populations. The vivipary is of obvious selective advantage under present climatic conditions as no *Deschampsia* of the *D. cespitosa* group has been found with ripe seed above about 600 m, and at 1000 m non-viviparous culms are often killed by frost before the anthers have been extruded. It would therefore appear that today, above about 600 m, non-viviparous plants can only spread by tillering and the occurrence of large circular clonal patches at high altitudes (conspicuous on the Ben Alder plateau and Ben Nevis) supports this suggestion. Although both diploids and tetraploids can produce occasional viviparous panicles late in the growing season, it would appear that only the tetraploid has been capable of producing regularly viviparous genotypes.

It thus seems that the southern viviparous type should be considered as belonging to the same species as the seminiferous tetraploid from which it is presumed to have repeatedly evolved. In contrast, the northern viviparous variant has no seed bearing counterpart in Britain, is morphologically distinct from *D. cespitosa* and should be considered a distinct species.

### Seminiferous variants

As discussed above, the seminiferous plants associated with the northern viviparous variant are nearly always diploid and confirm the findings of Rothera and Davey (1986). Counts by HMcA on plants from Orkney and Shetland (and Rothera & Davey (1986) from Shetland) remote from any viviparous plants are also diploid as are all counts from Iceland (Kawano, 1966). Elsewhere, the majority of reports are of diploids (Albers, 1980, Lawrence, 1945), but there are occasional reports of seminiferous tetraploids from N. America (Kawano, 1963, Hedberg, 1967, Johnson &

Packer 1968), Central Europe (Albers, 1980), the Pyrenees (Rothera and Davey, 1986) and Turkey.

Rothera and Davey (1986) report diploids scattered throughout England and Wales, largely in or near areas of known or suspected ancient woodland. They also report the tetraploid to be the commoner cytotype, especially on roadsides and recently colonised habitats. This suggests that in England and Wales, and perhaps South Scotland, diploids might be confined to shaded woodland habitats. In contrast, in the Scottish Highlands north and east of the Loch Lomond and the Loch Etive region, diploids occur on the mountain summits and at low altitudes in the northern isles.

*Southern Diploid*

To test the hypothesis that the southern diploids are woodland plants, four areas were examined in detail in the autumn of 1986.

1. Wooded banks of the River Ayr in South West Scotland (Grid ref. NS355214)
2. Wooded banks of the River Wharfe in Yorkshire between Barden and Bolton Abbey. (Grid ref. approx. SE076542)
3. Wooded gullies and moorland around Eldwick, near Bingley in Yorkshire (Grid ref. SE124407).
4. Savernake Forest in Wiltshire (Grid ref. SU/23-65-).

In all four areas, diploids were found only in shade, and often quite deep shade, in woodland on clay, in association with species such as *Mercurialis perennis, Sanicula europaea, Bromopsis ramosa* and *Schedonorus giganteus*. This association, together with the steep river or streamside topography in the first three cases, make it probable that these are habitats which have never been completely cleared of trees or scrub though they have all been disturbed to a greater or lesser extent by Man. At each site, tetraploid typical *D. cespitosa* was found in more open habitats within one to five metres of the diploid woodland variant.

In Wharfedale the *Deschampsia* of unshaded roadsides is tetraploid and grows in very close proximity to the diploid, the only cytotype present within the woodland. Similarly, in the Eldwick area, the diploid was only found on a very shady, steep bank under hazel by a small stream while, a metre or so above, on the sides of a lane, were tetraploids which also occurred on moorland and in a more open wood nearby. In Savernake forest diploids were found in shady situations while a tetraploid occurred on the edge of a grassy clearing in the picnic area, but within a few metres of a diploid clump.

It was surprisingly easy in all four widely separated areas to separate diploids from tetraploids in the field. The diploids had small spikelets often rather spaced out in open panicles which appeared delicate and somewhat resembled panicles of an *Agrostis*. The tetraploids on the other hand had larger spikelets with a tendency to be clumped together giving a totally different appearance to the panicle. The foliage of the diploids was a bright green whereas that of the tetraploids was bluish green and this difference was maintained in cultivation. As these differences appeared to be maintained over such distant sites they are likely to be generally applicable.

Thus it would seem that in Britain south of the Scottish Highlands morphologically differentiated diploids and tetraploids occupy different habitats. The diploids are found in shade in woodlands on clay and the tetraploids in open situations, whether on high ground, by the sea, or in ruderal habitats. It remains to be seen whether the lowland diploid can invade recently wooded areas or whether it is more or less confined to ancient woodlands.

In N. Scotland (v.c.96) a few isolated populations of *D. parviflora* have recently been found (Amphlett, 2019). These were in woodland, typically on flushed ground under *Alnus glutinosa*. Characteristic associated species include: *Ajuga reptans, Blechnum spicant, Carex laevigata, Carex remota, Chrysosplenium oppositifolium, Circaea x intermedia, Crepis paludosa, Dryopteris affinis* agg*., Dryopteris dilatata, Geranium robertianum, Lysimachia nemorum, Oreopteris limbosperma, Oxalis acetosella, Stellaria holostea, Stellaria nemorum, Veronica chamaedrys* and *Veronica montana*.

In British and Irish Floras, this taxon with small spikelets was first mentioned (at varietal level) in the first edition of the *Flora of Great Britain and Ireland* (Clapham *et al.*, 1952) and Hubbard (1954). However, it was not until the more detailed account in the Plant Crib (McAllister, 1988), that this taxon became more widely known. Rothera & Davy (1968) did not differentiate this diploid morphologically, considering it together with the northern diploid of the Scottish Highlands, although Grime *et al.* (1988) conclude that "diploids are mainly restricted to semi-natural woodland". Amphlett (2019) reviews identification features of *D. parviflora*.

*Northern diploid*

North and east of the Loch Lomond - Loch Etive - Crianlarich area in the south-west Scottish Highlands, seminiferous *Deschampsia* on mountains and in the Hebrides and Northern Isles are diploid while tetraploids have been found only in some low altitude and ruderal habitats (Rothera and Davey, 1986). These northern diploids are as yet morphologically indistinguishable from tetraploids in the field, although under cultivation they have shorter leaves and culms than the much more vigorous tetraploids.

Further south in the south west Scottish Highlands, central and southern Scotland and England, where the tetraploid is clearly native from sea level to the mountain summits, there is evidence of relic occurrences of the Northern diploid type. For example, on Cronkley Fell in Teesdale (Grid ref. NY844285) two diploids of the northern type were found growing on the sugar limestone on the summit of the fell alongside the *Gentiana verna* and *Helianthemum oelandicum subsp. levigatum*, species presumed to have closely followed the retreating ice at the end of the last glaciation. Occasional tetraploids occur in the same habitat (possibly introduced by Man), but otherwise the nearest tetraploid *Deschampsia* is 2 km distant and 150 m lower on the banks of the River Tees. It would seem that the diploid on the summit has been isolated by the surrounding bog, heather moor and cliff (and forest in earlier times) through which the tetraploid has not, until recently, been able to penetrate. On all other upland sites in Northern England only tetraploids have been detected.

Viviparous triploids, which on morphological grounds are probably hybrids between diploid and tetraploid plants of *D. cespitosa,* have been found on Beinn Mhor in Cowal near Dunoon (Grid ref. NS106907) and Ben Bhuidhe at the head of Loch Fyne, (Grid ref. NN204186) within the area in which all seed-bearing

*Deschampsia* appear to be tetraploid. The presence of these triploids suggests the former presence of the Northern diploid, which has now been replaced by the tetraploid.

*Seminiferous tetraploids*
Early counts on collections of seminiferous plants associated with viviparous ones showed that the tetraploid seminiferous plants occurred in native habitats in the upland areas of North Wales, Northern England, the Southern Uplands of Scotland and a clearly defined enclave of the South-West Scottish Highlands. Later counts showed the tetraploid to be the only cytotype present in a range of natural open habitats down to sea level within this area. Rothera and Davey (1986) have shown that the tetraploid is widespread in England and Wales, being the common cytotype of all but shaded and probably ancient woodland habitats.

## Taxonomy

There are five variants of the *D. cespitosa* complex in Great Britain and Ireland:
three seminiferous:
(a) southern woodland diploid - *D. parviflora*
(b) northern diploid - *D. cespitosa*
(c) widespread tetraploid - *D. cespitosa*
and two viviparous:
(d) southern - *D. cespitosa*
(e) northern - *D. alpina*

## Key to species of the *Deschampsia cespitosa* complex in Great Britain and Ireland

1a Panicles at least partially viviparous - - - - - - 2
1b Panicles seminiferous - - - - - - - - 3

2a Plant small, often less than 30 cm, leaf tip strongly hooded (cucullate). Panicles usually elongate-triangular in outline and secund when well grown, usually with reflexed branches; nearly always (in northern Europe) totally viviparous; plantlet attachment very brittle, glumes and lemmas closely appressed to plantlet, plantlet more than 0.8 mm in diameter below lowest true leaf.
***D. alpina***
2b Usually larger, leaf tip gradually tapered to sharp point. Panicle ovoid-triangular, not secund, rarely with reflexed branches, totally or partially viviparous, plantlet attachment firm, glumes and lemmas often divergent, plantlet usually less than 0.8 mm. in diameter below lowest true leaf.
***D. cespitosa*** (viviparous forms)

3a Leaves bright green, slightly scabrid on adaxial ridges, papillae on the flat surfaces of the adaxial ridges of the leaf appearing as indistinct or translucent, yellowish green spots (at x20 in living material). Spikelets small 2.5-3 (-3.5) mm. long, hairs at base of rachilla shorter than rachilla, hairs on rachilla less than half rachilla length. Plant of shady woodland.
***D. parviflora***

3b Leaves bluish, mid or dark green on adaxial leaf surface, coarsely scabrid on adaxial ridges, papillae on flat sides of ridges on adaxial surface of leaf appearing as opaque whitish green spots (at x20 in living material). Spikelets 3.5 mm. or more in length, hairs at base of rachilla usually longer than rachilla, hairs on rachilla more than half rachilla length. Plant of open habitats or thin woodland.

***D. cespitosa***

**Northern viviparous variant.**
***Deschampsia alpina* (L.) Roem. & Schult.**

*Aira alpina* L.
*Aira cespitosa* Linn. var.1 sp. pl. (1753)
*A. laevigata* J.E. Smith, in Sowerby, English Botany 30: No. 2102 (1810)
*D. cespitosa* subsp. *alpina* (L.) Tzvelev in Fedorov, Fl. Part. Eur. URSS 1: 209 (1974)

The northern viviparous variant is quite distinct. The markedly cucullate (hooded) leaf tips distinguish it from viviparous *Deschampsia* of the southern variant and almost all seminiferous plants in Great Britain and Ireland. This, together with the other morphological and behavioural characters mentioned in the key, suggest that it is a separate species quite distinct from *D. cespitosa.* (Figs. 2, 3 & 4).

**Figure 2. *Deschampsia alpina*. North facing Coire of Ben Cruachan, v.c.98, showing habitat and panicle barely emerged from sheath.
Image: H. McAllister. 5 August 1973**

This northern viviparous variant is usually referred to *D. alpina* (L.) Roemes & Shultes, based on *Aira alpina* of Linnaeus. Only in Great Britain has there been confusion with the name *D. alpina* also being applied to what are here interpreted as viviparous forms of *D. cespitosa*.

**Figure 3.** ***Deschampsia alpina*. Cultivated plant from Lochnagar, South Aberdeenshire, v.c.92, Scotland, showing typical short leaves. Image: H. McAllister**

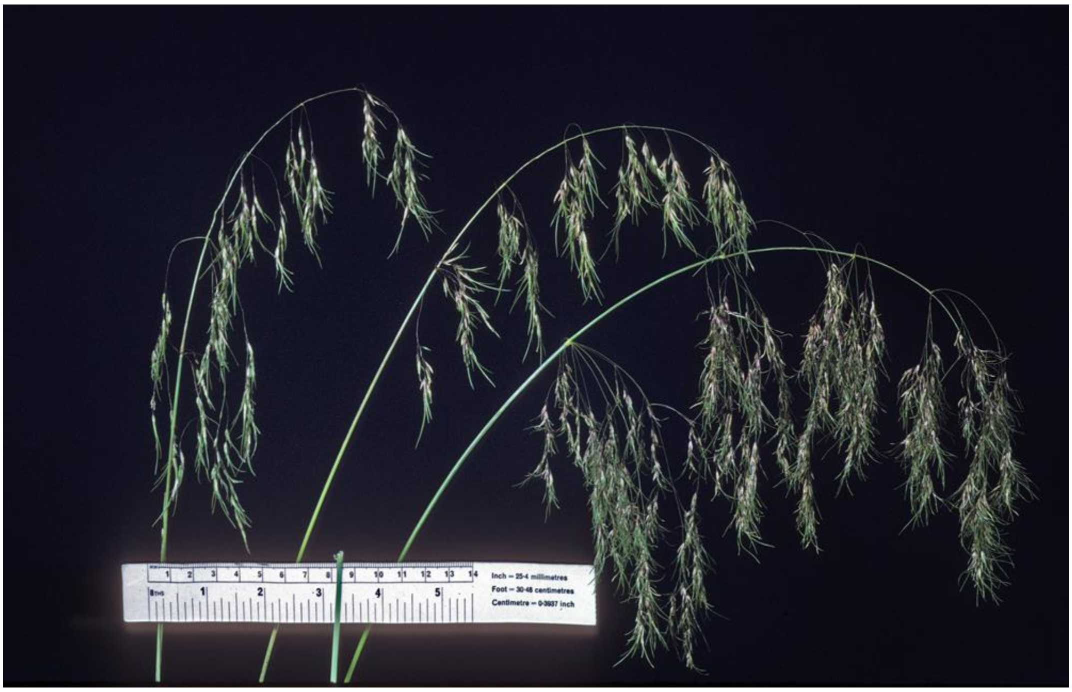

**Figure 4.** ***Deschampsia alpina* and *D. cespitosa*. Two panicles to the left show typical form of *D. alpina* from N.W. Highlands and Ben Nevis region (Scotland) with narrow, secund panicles with reflexed branches and large spikelets. Single panicle to right, of the viviparous form of *D. cespitosa* with smaller spikelets. Image: Norman Tait**

The confusion in Great Britain has arisen because of the presence of viviparous forms of *D. cespitosa* and the use of the position of insertion of the awn as the character distinguishing the species, near lemma base in *D. cespitosa,* above middle of lemma in *D. alpina* (Clapham *et al.*, 1962; Clarke, 1980). Viviparous plants of *D. cespitosa* show the whole range of variation from spikelets with well-developed florets and dorsally inserted awns to spikelets with no florets and the lowest 'lemma' being a miniature leaf. *D. alpina* is much more constant in that each spikelet usually has two florets, the lower being smaller than the upper. Note that in McAllister (1988, 1998) this taxon is referred to as *D. laevigata* (Sm.) Roem. & Schult..

### ***Southern woodland diploid*** ***Deschampsia parviflora*** **(Thuillier) Rohlena**

*Aira parviflora* Thuillier Flora Env. Paris, ed. 2.1: 38 (1799)
*D. parviflora* (Thuillier) Rohlena, Sitzungsber, Konigl, Bohm. Ges. Naturw., Math. - Nat. Cl. 1901 (23): 6 (1901).
*D. parviflora* (Thuillier) P. de Beauvois Agrost. 91. 160 (1812)

The southern woodland diploid is a distinct taxon (Fig. 5). Now that, in Britain at least, characters have been found which can distinguish it reliably from *D. cespitosa,* both vegetatively and in flower, with some degree of certainty, it is perhaps desirable to recognise it at a higher level.

It was recognised, at variety level, in some standard works (Clapham *et al.,* 1952, 1962, Hubbard, 1954, 1984), but not in Clarke 1980. Since 1991 it has been recognised at subspecific level as *D. cespitosa* subsp. *parviflora* (Thuill.) Dumort. (Stace, 1991). However, the authors believes this taxon to be at least as distinct as *Agrostis canina* is from *A. vinealis* or *A. gigantea* from *A. capillaris*. At the specific level it would become *D. parviflora* (Thuillier) Rohlena. In Britain it would be useful to recognise it as a distinct species as it is morphologically, ecologically and cytologically distinct from surrounding related *Deschampsia cespitosa*. As the surrounding *Deschampsia* of open ground is almost always tetraploid, this suggests that the woodland diploid will not normally interbreed with it and the two cytotypes will behave as quite separate breeding populations. In N. Scotland, Amphlett (2019) reported occasional intermediate plants that could not be determined as *D. parviflora* or *D. cespitosa*. It is possible that local *D. cespitosa* plants are the diplod, increasing the likelihood of hybridisation, though this has not been confirmed.

Occasional gene exchange between related diploids and tetraploids has been reported in *Campanula* (Bielawska, 1964) and *Betula* (Anamthawat-Jonsson & Tomasson, 1990)) and is most frequently in the direction diploid to tetraploid. This leaves the diploid uncontaminated and probably distinct even from triploids and interbred tetraploids. No such triploids have been found in association with *D. parviflora.*

In the most recent treatment of the complex in the whole of Europe Clarke (1980) makes no reference to the small-flowered woodland variant of *D. cespitosa* while recognising several northern variants as subspecies. In lowland Central Europe where tetraploid *D. cespitosa* s.s. is not known to occur, woodland diploids are likely to be surrounded by diploid *D. cespitosa* with which they might interbreed. However, Frey (1984), in a study of the complex in Poland, recognised the two taxa as distinct at the subspecific level, and Chiapella (2000) in his review of the *D. cespitosa* complex in central and northern Europe, recognised this taxon (as subsp. *parviflora*) as occurring in central Europe as well as in Great Britain.

**Figure 5. *Deschampsia parviflora*. Typical tussocks of bright green, narrow leaves, in woodland. Ferness (River Findhorn) (v.c.96). June 2017. Image: A. Amphlett**

## Northern seminiferous diploid, seminiferous tetraploid and southern viviparous tetrapoloid
## *Deschampsia cespitosa* (L.) P. de Beauvois

*Aira cespitosa* L Sp. Pl. (1753)
*D. cespitosa* (L.) P. de Beauvois Agrost. 91, 160 (1812)

Having distinguished the northern viviparous tetraploid variant as *D. alpina* and the southern lowland woodland diploid as *D. parviflora* , we are left with the northern seminiferous diploid and the large tetraploids, both seminiferous and viviparous. As discussed earlier, the taller viviparous tetraploid is no more than a series of viviparous variants, probably selected out of local tetraploid seminiferous populations. Unfortunately, no way has yet been found to distinguish morphologically between the tetraploid and the northern diploid, although the diploid does tend to be smaller. It therefore seems best to refer to them simply as diploid and tetraploid seminiferous, and tetraploid viviparous *D. cespitosa.*

**Geographical distributions within Great Britain and Ireland?**
*Deschampsia cespitosa* agg. is ubiquitous, at the hectad scale, across Great Britain and Ireland (Fig. 6).

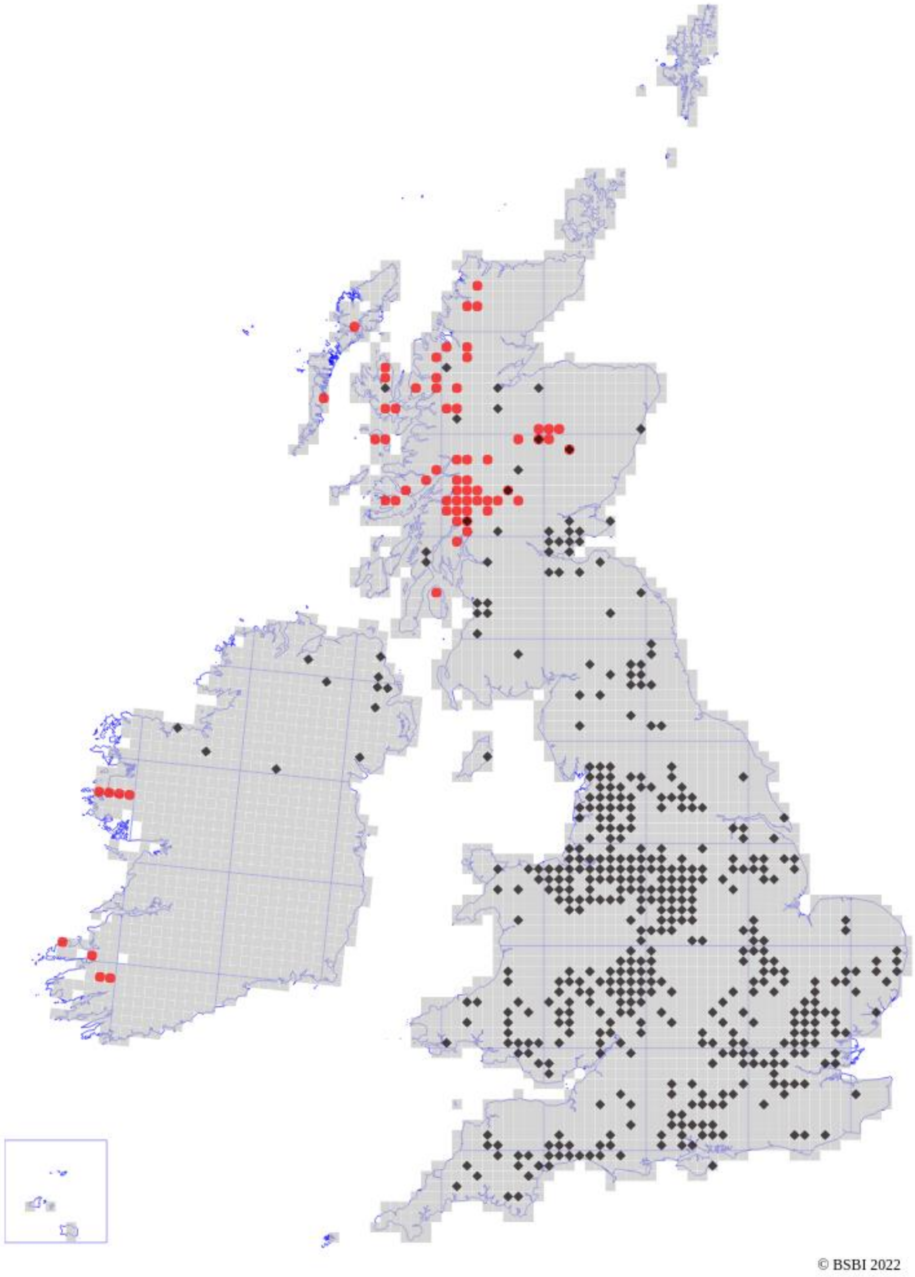

**Figure 6. Distribution of *Deschampsia cespitosa* agg. (grey squares), *D. alpina* and hybrids (red circles) and *D. parviflora* (black diamonds). From BSBI distribution database 15 June 2022**

### *Deschampsia alpina*

The British distribution of *D. alpina* (Figs. 6, 7 & 8) is similar to that of several other alpines such as *Carex saxatilis, Sibbaldia procumbens* and *Cerastium nigrescens*. This distribution is consistent with it being a relict of the glacial period when it probably survived close to the ice margins and spread northwards following the retreat of the ice to attain its present distribution in open, moist, high mountain habitats. Its habitats today in Iceland, Greenland and Norway are probably similar to those in Britain during the last glaciation.

In Great Britain this taxon is listed as Data Deficient (Cheffings *et al*., 2005, revised Feb 2021). There are no confirmed records from England or Wales. In Ireland this taxon is on the Waiting List (Wyse Jackson *et al*., 2016).

**Figure 7. *Deschampsia alpina* (red dots). Populations sampled (grey dots). Two locations in Ireland (Brandon & Mangerton Mts., Kerry) are not mapped**

The identification features of *D. alpina* were only clarified in McAllister (1988). Earlier records may include misidentifications eg. of hybrids between *D. alpina* and the diploid northern seminiferous *D. cespitosa*. As mentioned, above, such plants from South Uist in the Outer Hebrides, Glen Coe, the Ben Alder area and Mull are triploids and are presumably hybrids between the tetraploid northern D. alpina and the diploid northern seminiferous *D. cespitosa.* These closely resemble *D. alpina*. Some records of *D. alpina* from the south-western part of its British range might refer to viviparous tetraploid *D. cespitosa*.

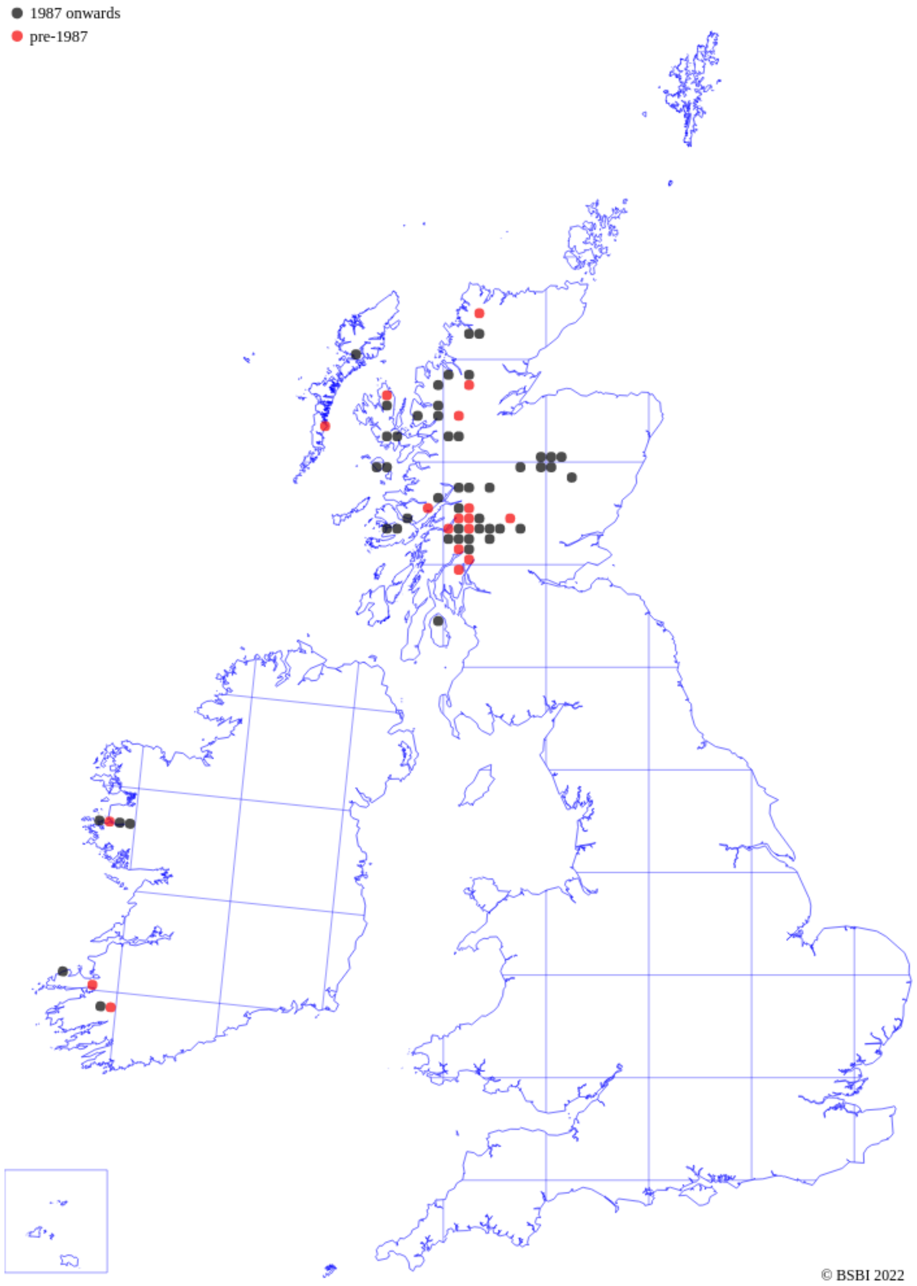

**Figure 8. Hectad distribution of *D. alpina* from BSBI Distribution database (accessed 19 February 2022). Black circles 1987 onwards, red circles pre-1987. Some hectad records with only pre-1987 records may be errors.**

### *Deschampsia parviflora*

In Great Britain, *D. parviflora* is widespread north to the Scottish central lowlands, with a few sites in the Highlands and Aberdeen. It is apparently rare in Ireland, where it was first reported in 1967/1968 (Farragher, 1969). In N. Ireland, it has been reported from several localities since 2005. (Figs. 6 & 9)

**Figure 9. *Deschampsia parviflora* (red dots). Populations sampled (grey dots)**

### *Deschampsia cespitosa* - diploid

No other species seems to have a similar distribution (Fig. 10) to this cytotype of *D. cespitosa,* though the Scottish part of the distribution of *Drosera anglica* resembles it closely even to the absence of both in the south-west Scottish Highlands. The occurrence of this cytotype from sea level to high altitudes in the islands and isolated northern areas and its confinement to mountains further south seems to be a relict distribution, this cytotype only surviving where the tetraploid has not been able to penetrate. Competition with the morphologically and ecologically almost identical tetraploid cytotype, which is presumably more competitive, may have confined it to its present distribution area.

**Figure 10. *Deschampsia cespitosa* - diploid (red dots). Populations sampled (grey dots).**

### *D. cespitosa* - tetraploid

The distribution of the tetraploid cytotype of *D. cespitosa* (Fig. 11) is rather similar to that of *D. parviflora* but extends further north into the south-west Scottish Highlands at all altitudes and at low altitudes into the central, eastern and northern Highlands. It also occurs in Ireland. As with *D. parviflora,* its distribution in a single, more or less continuous block and absence from the periphery of northern Scotland suggest a relatively recent spread through Britain with occasional further spread, probably by human activity. Species with similar distributions include *Hypericum perforatum*, *H. maculatum*, *Alliaria petiolata* and *Lysimachia vulgaris.*

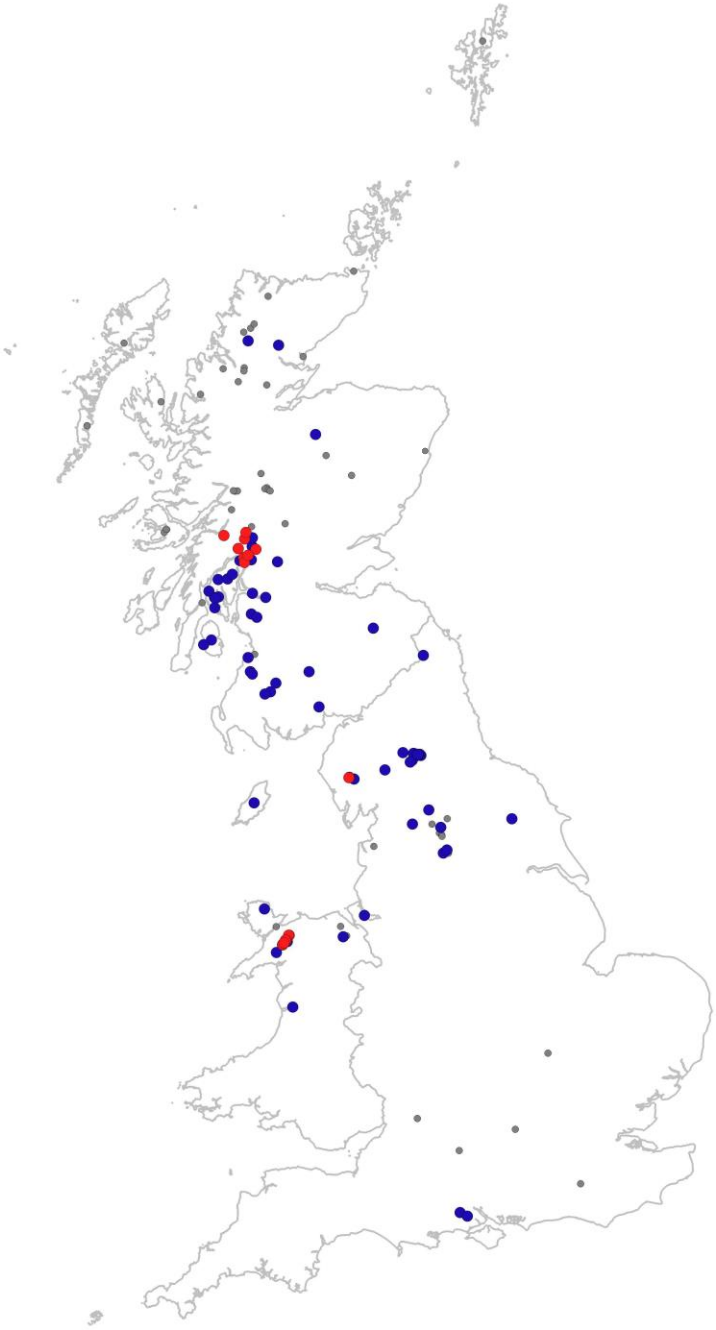

**Figure 11.** ***Deschampsia cespitosa*** **tetraploids. Viviparous (red dots). Seed-bearing (blue dots). Populations sampled (grey dots).**

## World geographical distributions

*D. alpina*

Collections from Ireland, Greenland, Iceland and Norway have been studied in cultivation and all conform to the concept of *D. alpina* obtained from plants in Scotland. There is some variation, with Greenland plants being smaller and less vigorous than others, but all have the very brittle spikelets with connivent glumes and cucullate leaf apices characteristic of the species.

Almost all viviparous herbarium specimens collected outside Britain also appear to be *D. alpina,* including one outside the range given by Hulten (1958). This is a specimen from the Bodensee in Germany which is usually referred to *D. rhenana*

Gremli (Kawano, 1963; Albers, 1978). This outlying locality is very isolated from the main distribution of the species but it could be a relict station of *D. alpina*. Similar disjunctions in the distribution of primarily arctic species are known, e.g. *Betula nana* and *Sabulina stricta* (Jalas & Suominen 1983).

The distribution given by Hulten (1958) extends from a few localities on the western arctic Canadian seaboard through Greenland, Iceland, Britain, Scandinavia, Spitzbergen and Novaya Zemlya into the arctic seaboard of Central Siberia with outlying stations on Wrangell Island and the adjacent mainland of arctic Eastern Siberia.

Seminiferous herbarium specimens which are referable to *D. alpina* (H. McAllister, personal observation) have been collected within the distribution range of the viviparous variant in Greenland and south and west of the occurrence of viviparous plants in Labrador, Newfoundland and Ungava Bay. Kawano (1963 p. 727) reported a plant with 2n=49 from Gaspé, Quebec, Canada (which he named *D. cespitosa subsp. littoralis*). A photograph of the specimen in Kawano's paper appears to agree with *D. alpina.* In 2010 seed of this was collected on Mt. Serpentine in the Parc National de la Gaspésie and proved to be tetraploid with 2n=52. (Fig. 12).

**Figure 12. *Deschampsia alpina* – Cultivated tetraploid seed bearing plant from Mt. Serpentine, Parc National de la Gaspésie, Quebec, Canada. Note narrow leaves, which were much less obvious in the wild plant Image: H. McAllister.**

It is likely, therefore, that the seminiferous plants with large spikelets, triangular panicles, and often with reflexed lower panicle branches, from Greenland, Labrador, Gaspé Peninsula, Newfoundland and Ungava will be tetraploid and should be regarded as the seminiferous variant of *D. alpina.*

A seminiferous tetraploid from Lac de Joux in Switzerland kindly given by Dr. Albers of Westfälische Wilhelms-Universität, Munster, (as *D. littoralis* (Gaudin) Reuter) has the open tussock habit and cucullate leaf tip of *D. alpina* though it is taller growing than the arctic plants. This also should probably be refered to *D. alpina*.

HMcA has not seen viviparous herbarium specimens from NE America or N. Asia, but the distribution given by Hulten (1958) is likely to be more or less correct. The main question mark hangs over disjunct records such as those from the Wrangell Island region though, as Hulten implies in his map, this isolation may be more apparent than real due to our lack of knowledge of the flora or the arctic Siberian coast. However, it is possible that such plants could be viviparous races of local taxa not easily differentiated from *D. alpina* from herbarium specimens.

A very small triploid plant from Spitzbergen looked in cultivation like a viviparous variant of *D. brevifolia* R. Br. and bore little resemblance to *D. alpina*. If *D. alpina* occurs in Spitzbergen this plant could be a hybrid between the reportedly diploid *D. brevifolia* (Kawano, 1963) and tetraploid *D. alpina,* but as two thirds of the hybrid's genome would have come from *D. alpina* it would be expected to resemble that species more than it does. This 10 cm. tall plant with short narrow leaves and dense culms extending little above the leaves and plantlets usually require two seasons growth before producing culms, so may well be an autotriploid of *D. brevifolia.* Its vivipary is not a result of the conditions of cultivation as it was grown from plantlets collected in Spitzbergen.

*D. alpina* has a typical northern oceanic montane distribution in NE America, Greenland, Iceland, Great Britain and Ireland and Scandinavia, and it does not extend into the more arctic regions of N. America and the northern part of Greenland where the drier climate would presumably be less favourable for the establishment of the viviparous plantlets. If the records from Spitzbergen, Franz Joseph Land, Novaya Zemlya and arctic Siberia are referable to the same species, then it extends into a much more arctic climate in this area.

### *D. parviflora*

Little is known in detail about the distribution of *D. parviflora* outside Britain but, from its restriction in Britain to damp shaded woodland habitats, it would be expected to occur in similar habitats throughout Continental Europe (Frey, 1984). It was the only species of the *D. cespitosa* complex found by HMcA throughout the province of Mecklenburg in north east Germany where it occurred on clay and chalk, largely in woodland.

The 'Plants of the World' online database (Kew, accessed 18 February 2022) lists *D. parviflora* as occurring in the following areas: Baltic States, Belarus, Belgium, Bulgaria, Central European Russia, Czechoslovakia, East European Russia, France, Germany, Great Britain, Hungary, Italy, North Caucasus, North European Russia, Northwest European Russia, Poland, Sweden, Ukraine, West Siberia.

Very similar diploid plants with spikelets up to 4mm were collected by HMcA in woodland on heavy clay at Listvyanka on the south western shores of Lake Baikal in Siberia

*D. cespitosa*

Diploid *D. cespitosa* is presumed to be the commoner cytotype worldwide, with the typical state and numerous (at least 40 according to Hulten, 1964) varieties having a circumboreal distribution in damp habitats in arctic and temperate regions throughout Eurasia and N. America, with outlying stations in North, Central and South Africa, New Guinea, Australia and New Zealand, and probable introduced occurrences in S. America. Whether or not all these plants belong to *D. cespitosa s.s.* of western Europe awaits further study.

In Britain diploid *D. cespitosa* appears to be the only cytotype present in Orkney, Shetland, the Outer Hebrides and perhaps the adjacent mainland, and at high altitudes throughout the Highlands except in the South West. Away from these geographically peripheral parts of northern Scotland almost all *D. cespitosa* in the main island of Great Britain is tetraploid.

The same diploid taxon has been reported from Iceland (Kawano, 1966 and this study), Finland (this study) and these European plants are very similar to diploids collected by HMcA from unshaded flushed habitats in south east Tibet. Diploids from the Rocky Mountains and further west in North America look superficially very similar but behave differently in cultivation in England, dying back completely in winter and often failing to regrow the following spring.

As no morphological means has yet been found to distinguish reliably between diploids and tetraploids and relatively few chromosome counts have been made from areas where tetraploids are likely to occur, it is not possible to give very accurate distributions for the two cytotypes outwith Great Britain. Tetraploids have been found in western France in Normandy, Brittany and the Pyrenees (Kerguélen, 1987 and this study) and in Turkey. Morphologically these plants resemble British tetraploids and there can be no doubt that the French populations are part of the same taxon as the British ones. It has been suggested that the Turkish plants might belong to a different taxon, but they are very similar to those from western Europe though they tend to be of greater stature. Such disjunct distributions with species occurring in Turkey and western Europe, but not in the intervening areas are known (Hedge, 1986), e.g. *Rhododendron ponticum* and *Dryopteris aemula*, so it is not improbable that the Turkish tetraploid *D. cespitosa* populations could be referable to the same taxon as tetraploids in western Europe. Until more information is available on plants in intervening areas we cannot be certain that the disjunction is as great as appears at present.

Viviparous populations of *D. cespitosa*, tetraploid and rarely triploid, are known only from Britain. The occasional production of viviparous panicles in otherwise seminiferous individuals or daylength induced vivipary in otherwise seminiferous individuals (Lawrence, 1945; Nygren, 1949; Kawano, 1966) is known from elsewhere.

## Phytogeography

The distribution of tetraploid *D. cespitosa* in Britain is unusual and interesting. It appears to occur to the almost total exclusion of the diploid (excepting *D. parviflora*) throughout England, Wales, the Southern Uplands and Lowland Scotland and the small enclave of the South West Scottish Highlands around Arrochar, Crianlarich and Oban. The occasional occurrence of diploid (Cronkley Fell, Teesdale) and triploid (Ben More Cowal and Ben Bhuide, both in south west Argyll) plants at high altitudes within this area suggests that the tetraploid may have replaced the diploid. (Reports of low altitude diploids or triploids could suggest confusion or hybridisation with *D. parviflora*).

There is a striking contrast in the *Deschampsia* flora between the mountains of the south-west Scottish Highlands around Arrochar, Loch Lomond, Glen Falloch, Crianlarich and Ben Cruachan and such mountains to the north and east as Ben Alder, the Ben Nevis range, the Cairngorms and the Northern Highlands. The contrast is particularly noticeable between such big grassy mountains as Ben Ime and Ben Cruachan in the south west and Aonach Beag of the Nevis range to the north. All three mountains have extensive *Deschampsia* grasslands to over 900 m with *D. alpina* occurring in wet open habitats at very high altitudes. However, whereas on Aonach Beag all the *D. cespitosa* is non-viviparous and diploid, on Ben Ime and Ben Cruachan viviparous tetraploid *D. cespitosa* occurs commonly from 525 m and 350 m respectively and is common among the non-viviparous plants at higher altitudes. Here all viviparous and non-viviparous plants are tetraploid. As the floras of these mountains, especially with respect to common species, are otherwise relatively similar, it would seem that a geographical rather than an environmental factor is likely to be responsible for the distribution found.

In Iceland *D. alpina* is one of the first colonisers in wet, open habitats following glacial retreat while diploid *D. cespitosa* is a principle component of the highest grasslands. It can therefore be postulated that these two taxa behaved similarly as the ice retreated in Britain at the end of the last glaciation. At some point the tetraploid presumably invaded and spread from the south, replacing the diploid. Now, if it had just reached as far as the Loch Lomond, Loch Fyne, Loch Awe lowlands by the climatic maximum (Atlantic period, Zone V, about 7,000BP) when the climate was at its warmest since the last glaciation and warmer than today, it would have been able to spread to the mountain summits by seed. Further northward and eastward spread would probably be hindered by dense forest developing in the lowlands, and in the mountains to the north and east it would be the diploid which ascended to the summits as the climate warmed. It is to be expected that the tetraploid would subsequently make some advances to the north and east at lower altitudes, especially with forest destruction through climatic cooling and Man's activities. The tetraploid could therefore be expected to occur at lower altitudes in the central and northern highlands and this is in fact what is found. However, as the present climate restricts seed production in Scotland in most years to altitudes of less than about 600 m, the tetraploid will not be able to replace the diploid at higher altitudes until climatic warming allows its dispersal to higher altitudes.

Though there would seem to have been (1966) little seed production much above 600 m, considerable areas of pure *Deschampsia* sward can be found above this altitude, up to the 1200 m plateau on Aonach Beag in the Nevis range. At progressively higher altitudes the panicles are killed by early frosts at progressively earlier stages, from unripe caryopses at 600 m to unopened flowers at 900 m and above. Such observations have been carried out in several seasons on several mountains from September through to the following April, when the previous season's panicles emerge from their overwinter preservation under the snow. It is therefore clear that both cytotypes migrated to their higher altitude sites when the climate was considerably warmer than it is today, perhaps in the climatic maximum about 7,000BP.

At high altitudes the occurrence of large circular patches, which are each clearly single clones, shows that many of these are very old plants. As in *Nardus stricta* with a similar wide altitudinal range, the population structure above the level of regular seed production is very different from that at lower altitudes. In the lowlands, areas of large tussocks, each of which appears on morphological grounds to be a discrete genotype, are surrounded by isolated tussocks each of which appears to have arisen from a separate seed as judged morphologically - individual genotypes are often recognisable through the different colouration and degrees of bunching of the spikelets in the panicles. At high altitude the habit is not so tussocky and quite large (up to 9 m in diameter) clonal patches are often evident, often in the form of circular patches broken up into arcs.

## Future work

*D. cespitosa* is not a cultivated species and is usually regarded as a weed (Szakacs-Nagy & Rotar, 1995). Its geographical distribution in undisturbed habitats is therefore likely to have been little affected by man. Even in disturbed habitats it is likely to be the locally present cytotype which will invade, though a foreign cytotype could be introduced as a contaminant if grass seed is sown. There is evidence that isolated areas such as islands were later to be invaded by colonising species than the mainland. For example, Boyd & Dickson (1986) found that *Corylus* did not become common on the island of Arran in the Firth of Clyde until about 500 years after its rise in frequency on the adjacent Scottish mainland in Ayrshire. It will therefore be instructive to see which cytotype(s) are found on the islands of Jura, Islay and Colonsay, on neighbouring mainland coasts, and in Ireland. It will be most important to sample such relatively undisturbed habitats as seaside cliff grasslands and mountain areas where the diploid may persist, but it will also be interesting to know which cytotype occurs on roadside verges and re-seeded grasslands to see if the tetraploid cytotype might have been recently introduced by man as may have happened on Cronkley Fell in Teesdale.

The finding of more relict diploid *D. cespitosa* within the area of the tetraploid would tend to support the hypothesis that the diploid has been replaced by the tetraploid. The most promising place to look would seem to be high summits in Teesdale and the South West Scottish Highlands, but islands such as Lundy, the Pembrokeshire islands and Holy Island in Northumberland might also have been inaccessible to a relatively recent coloniser.

As the viviparous tetraploids are often only partially viviparous and grow with seminiferous tetraploids it would seem to be an ideal subject for the research suggested by Elmqvist & Cox (1996) into the evolution of vivipary. In other viviparous species such as *Poa alpina* and *Festuca vivipara* chromosome number differences between the viviprous and seminiferous plants and apomixis complicate the relationship.

Within the general distribution area of *D. cespitosa* in Europe there are several quite distinct but aberrant populations which retain their integrity. Some of these have been described as distinct taxa (e.g. *D. cespitosa* subsp. *bottnica* (Wahlenb.) G.C.S. Clarke and *D. cespitosa* subsp. *paludosa* (Schübler & Martens) G.C.S. Clarke). Cultivation shows that these are truly distinct in their appearance and behaviour from *D. cespitosa.* Both are diploid. They may be more closely related to *D. alpina* as the bases of their tussocks consist of rather rigid divergent tillers, a high proportion of which produce culms, and the tussocks tend to have elongated lower internodes and so grow out of the ground and die off in cultivation in the same manner as seen in *D. alpina.*

Narrow leaved plants from the Sierra de Cazorla, Jaen province in south Spain are diploid but otherwise greatly resemble *D. cespitosa.* This variant has been referred to *D. meadia* (Gouan) Roemer & Schultes but there are doubts as to its distinctness (Bayer & Lopez, 1994). This diploid population is isolated from other diploids of the complex by the tetraploid populations of the Pyrenees.

Seminiferous diploid populations closely resembling dwarf *D. alpina* grow in shallow water in sheltered inlets on the shores of Lake Baikal. This very distinct taxon with many of the characteristics of *D. alpina* (hooded leaf tips and triangular panicles with reflexed branches) may be ancestral to tetraploid *D. alpina.* Comparison with herbarium specimens from northern Asia suggests that this diploid may be the taxon which is variably referred to *D. arctica* (Spr.) Schischr. (=*Aira arctica* Spreng.), *D. cespitosa* subsp. *borealis* (Trautv.) Tzvelev (=*S. borealis* (Trautv.) Kryl.), *D. sukatschewii* (Popl.) Roshev., *D. cespitosa* subsp. *obensis* (Roshev.) Tzvelev. (= *D. obensis* Roshov)*, D. cespitosa var. orientalis* Hulten in part, and *D. alpina* subsp. *kolgujewensis* R. Pohle.

The relationships among the above diploid entities and their relationships with the tetraploids of the complex would be instructive to investigate.

## Usefulness of members of the D. cespitosa complex

Although in Britain members of the *D. cespitosa* complex are usually regarded as weed grasses of no value, they are sometimes used as fodder and may have a future in reclamation work on difficult, wet sites.

In 1971 the HMcA saw a large barn full of *D. cespitosa* hay near Akureyri in northern Iceland. This was to be used primarily for feeding sheep. Although cattle are said not to like the roughness of the foliage, cattle roaming in the ancient gully woodlands of N. Wales in winter seem to eat the winter-green *D. parviflora* in preference to other species.

In winter on the sheep pastures of Teesdale and the North Welsh hills often the only grass to show obvious signs of having been grazed is *D. cespitosa*. That sheep eat *D. cespitosa* in preferance to other species is also suggested by the fact that, following the exclusion of grazing animals, predominantly sheep, *D. cespitosa* often becomes dominant where previously it was only a minor component of the sward. This can frequently be seen where areas are fenced for the planting of trees, though it is also evident in experimental exclosures on hill land above the treeline in Teesdale and at Moor House. This evidence suggests that, far from being a weed grass, *D. cespitosa* is a valuable fodder grass for sheep on wet hill land.

The frequency with which *D. cespitosa* dominates roadside and waste ground vegetation on wet soils shows that it is a successful and vigorous coloniser of bare ground and could therefore be considered for use in reclamation schemes. As it is a large, quick-growing species which can root deeply in cold, wet soils it could be useful for stabilising such soils. Its natural spread in the wild seems often to be restricted by lack of seed. The flowering culms are large and conspicuous and therefore grazed where there is any significant grazing pressure and, as it is a tufted species, vegetative spread is slow. No commercial source of seed is usually available.

## Acknowledgements

HMcA is very grateful to all those who sent plants, especially Dr. Albers, and the botanic gardens which sent seed through the Botanic Gardens Seed Exchange.Thanks are also due to the herbaria at Kew, the Natural History Museum and the Linnean Society for access to specimens and whose staff gave much assistance. Dr. R. Brummitt and Dr. S. Cafferty gave advice on Linnaen types and Mr. A. Chater on nomenclature and took great care in checking an early draft of the manuscript. HMcA should also like to thank Professor R. Marrs for helpful comments on the manuscript and the gardening staff at Ness Botanic Gardens for help in the cultivation of plants of limited horticultural interest. Finally, HMcA should like to thank his family for accompanying him on many *Deschampsia* hunts.

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ISSN: 2632-4970

https://doi.org/10.33928/bib.2022.04.314

## APPENDIX I
## List of localities from which chromosome counts have been obtained.

***Deschampsia alpina* 2n=52 or *c.*52**

Scotland, Mid Perth, Ben Lawers, NN63-41- (McAllister 6.1986), v.c.88
Scotland**,** Argyll, Arrochar, Ben Ime, NN255090 (Mc Allister 7.1972), v.c.98
Scotland, Mid Ebudes, Mull, Beinn nan Gabhar. NM546361 (McAllister 7.1968), v.c.103
Scotland, Mid Ebudes, Mull, Ben More. NM524334 (McAllister 14.7.1968), v.c.103
Scotland, W. Ross, Edidhe nan Glach Geala. NH259847 (McAllister 27.8.1968), v.c.105
Eire, Mangerton Mt. (McAllister 9.1970), v.c.H1 or v.c.H2

***Other localities confirmed morphologically from cultivated plants***

Scotland, S. Aberdeen, Lochnagar, 1050m. NO245858 (McAllister 8.9.1973), v.c.92
Scotland, Westerness, Nevis Range, Aonach Beag, 1200m. NN196715 (McAllister 17.8.1969), v.c.97

Scotland, Westerness, Ben Nevis, Coire Leis, 1050m. NN173713 (McAllister 19.8.1969), v.c.97
Scotland, Westerness, Creag Meagaidh, Glen Spean, 1020m. NN413875 (McAllister 7.8.1973), v.c.97
Scotland, Argyll, Ben Cruachan, Coire Dearg, 900m. (McAllister 5.8.1973), v.c.98
Scotland, W. Ross, Dundonnel, An Teallach, c1000m. NH065838 (McAllister 18.8.1966), v.c.105
Scotland, W. Ross, Braemore, Sgurr Mor Fannich, 990m. NH204719 (McAllister 17.8.1966), v.c.105
Scotland, E. Sutherland, Assynt, Conival, 960m. NC318210 (McAllister 28.8.1968), v.c.107
Scotland, Sutherland, Ben More Assynt, 960m. NC3--2-- (McAllister 28.8.1968), v.c.107 or v.c.108
Scotland, Outer Hebrides, Harris, Clisham, 786m. NB155074 (McAllister 28.8.1967), v.c.110
Scotland, Inverness, Cairngorm, 1125m. (McAllister 8.8.1973), v.c.94/96
Eire, S. Kerry, Brandon Mt., v.c.H1

***Deschampsia cespitosa***
**Seminiferous diploid 2n=26**
England, NW Yorkshire, Upper Teesdale, Cronkley Fell, Thistle Green. NY844285 (2 counts) (McAllister 6.1987), v.c.65
England, NW Yorkshire, Upper Teesdale, Cronkley Fell, Whitewell Green. NY839283 (McAllister 6.1987), v.c.65
Scotland, Westerness, Nevis Range, Aonach Beag, 1100m. NN196715 (McAllister 1978), v.c.97
Scotland, Westerness, Ben Nevis. NN159717 (McAllister 1978), v.c.97
Scotland, Westerness, nr. Ben Alder, Aonach Beag, 990m. NN457738 (McAllister 8.1970), v.c.97
Scotland, Westerness, Ben Alder, Coire Cheap, NN466745 (McAllister 10.1978), v.c.97
Scotland, Westerness, Ben Alder, 1000m. NN482725 (McAllister.8.1970), v.c.97
Scotland, Westerness, nr. Ben Alder, Beinn Eibhinn, 990m. NN449735 (McAllister 8.1970), v.c.97
Scotland, Argyll, Bridge of Orchy, Ben Dorain, 900m. NN326387 (McAllister 4.8.1973), v.c.98
Scotland, Kintyre, Tarbert, 10m. NR872688 (McAllister 8.1996), v.c.101
Scotland, N. Ebudes, Isle of Skye, The Storr, NG49-53- (S. & J. Sutton), v.c.104
Scotland, W. Ross, nr. Ullapool, Ben Dearg, 900m. NH256818 (McAllister 15.7.1973), v.c.105
Scotland, W. Ross, Torridon, Beinn Alligin, 750m. NG857603 (McAllister 17.7.1973), v.c.105
Scotland, E. Ross, Ben Wyvis, 900m. NH466689 (McAllister 16.7.1973), v.c.106
Scotland, E. Sutherland, nr. Dornoch. NH800950 (M. Birch 27.9.1987), v.c.107
Scotland, W. Sutherland, Ben Hope, 840m. NC478504 (McAllister 13.7.1973), v.c.108
Scotland, W. Sutherland, Inchnadamph, NC25-17- (McAllister 8.1973), v.c.108
Scotland, Caithness, Mey. ND26-73- (M. Birch 22.9.1987), v.c.109

Scotland, Outer Hebrides, South Uist, Beinn Mhor, NF81-31- (McAllister 5.1979), v.c.110
Scotland, Shetland, mid Yell. HU48 (W. Scott), v.c.112
Scotland, Inverness, Glen Spean, Creag Meagaidhe. 1020m (McAllister 1978), v.c.97

### Seminiferous tetraploid 2n=52 or *c.*52

England, S. Hampshire, New Forest, Boulder Wood (=Bolderwood). SU242085 (McAllister 1987), v.c.11
England, S. Hampshire, New Forest, Hollands Wood. SU309052 (McAllister1987), v.c.11
Wales, Cardiganshire, Cwm Llyfnant. SN705973 (A. Chater), v.c.46
Wales, Carnaervon, Glyders, Devil's Kitchen, 660m. SH638588 (McAllister 22.11.1973), v.c.49
Wales, Carnaervon, Glyders. SH65-57- (McAllister 1975), v.c.49
Wales, Carnaervon, Snowdon, Clogwyn y Garnedd, 1005m SH611545 (McAllister 1974), v.c.49
Wales, Carnaervon, Cwm Llefrith. SH55-47- (McAllister 1975), v.c.49
Wales, Denbighshire, Moel Famau, 300m. SJ168619 (McAllister 1974), v.c.50
Wales, Anglesey, Parc Mine, SH44-87- (McAllister 6.1987), v.c.52
England, Cheshire, Eastham Woods. SJ363815 (McAllister 1987), v.c.58
England, NE Yorkshire, Malton, Castle Howard. SE718703 (McAllister1987), v.c.62
England, SW Yorkshire, Bingley, St. Ives. SE088388 (2 plants) (McAllister, 12.1986), v.c.63
England, MW Yorkshire, Settle. SD80-65- (McAllister 1974), v.c.64
England, MW Yorkshire, Wharfedale, Trollers Ghyll. SE06-62- (McAllister 12.1974), v.c.64
England, MW Yorkshire, Buckden Pike, SD9578 (McAllister 5.1982), v.c.64
England, MW Yorkshire, Bingley, Eldwick, Nicholson's Wood, SE121416 (2 plants) (McAllister 10.1986), v.c.64
England, MW Yorkshire, Bingley, Eldwick, Beck Bottom, (McAllister 10.1986), v.c.64
England, NW Yorkshire, Upper Teesdale, Cronkley Fell, Thistle Green, 537m. NY844285 (3 plants), NY846285 (McAllister 13.8.70), v.c.65
England, NW Yorkshire, Upper Teesdale, Cronkley Fell, Whitewell Green. NY839283, v.c.65
England, NW Yorkshire, Upper Teesdale, Mickle Fell, 750m. NY803241 (McAllister 18.9.70), v.c.65
England, NW Yorkshire, Upper Teesdale, High Force, NY882285 (Mc Allister 6.1987), v.c.65
England, Co. Durham, Upper Teesdale, Widdybank Fell. NY81-30- (McAllister 20.5.70), v.c.66
England, Co. Durham, Upper Teesdale, NY873295 (McAllister, 6.1987), v.c.66
England, Co. Durham & NW Yorkshire, Upper Teesdale, Cronkley Fell, NY862295, 856294, 845296, 854295 (12 plants) (McAllister 6. 1987), v.c.66 & v.c.65
England, N. Northumberland, Cheviot. NT9020 (McAllister 1971), v.c.68
England, Westmorland, Langdale Pikes, 120m. NY268068 (McAllister 14.3.1971), v.c.69
England, Westmorland, Knock Fell. NY717311, v.c.69

England, Westmorland, nr. Shap, Wet Sleddale. NY552152 (McAllister 10.1974), v.c.69
England, Westmorland, Knock Fell, 223m. (9.10.70), v.c.69
England, Westermorland, Upper Teesdale, Little Fell, 732m. NY784224 (McAllister 18.9.70), v.c.69
England, Cumberland, Great End, NY2208, 750m. (McAllister 8.10.70), v.c.70
Isle of Man, Lonan, Glen Roy, Ballalheannagh, 240m. SC3--8-- (McAllister 1987), v.c.71
Scotland, Dumfries, nr. Thornhill, NS85-05- (4 plants) (McAllister 12.1987), v.c.72
Scotland, Kircudbrightshire, Corserine, 780m, NX500870 (McAllister 2.1969), v.c.73
Scotland, Kircudbrightshire, The Merrick, 600m, NX4--8-- (McAllister 1.6.1968), v.c.73
Scotland, Kircudbrightshire, Kendoon. NX5--9-- (McAllister 12.1974), v.c.73
Scotland, Kircudbrightshire, Cargenbridge, Carruchan. NX946731 (McAllister 12.1974), v.c.73
Scotland, Ayrshire, nr. Kilbirnie, Ladyland. NS32-58- (McAllister 12.1974), v.c.75
Scotland, Ayrshire, Beith, Lochlands Hill. NS37-55- (McAllister 1978), v.c.75
Scotland, Ayrshire, Heads of Ayr. NS29-18- (McAllister 1978), v.c.75
Scotland, Ayrshire, Crosshill, Rowantree Farm. 26/315055 (McAllister 1986), v.c.75
Scotland, Ayrshire, Crosshill, Cloyntie Farm. NS333033 (McAllister 1986), v.c.75
Scotland, Midlothian, Stow. NT44-45- (M. Birch 8.1987), v.c.83
Scotland, W. Perth, nr. Aberfoyle, Lendrick NN5606 (M Birch 91987), v.c.87
Scotland, W. Perth, Inverarnan. NN332206 (McAllister 8.1974), v.c.87
Scotland, M. Perth, Tyndrum. NN334285 (McAllister 1974), v.c.88
Scotland, Moray, Carrbridge. NH91-23- (M. Birch 28.9.1987), v.c.95
Scotland, Argyll, nr. Invereray, Beinn Bhuidhe. 900m. NN204186 (3 plants) (McAllister), v.c.98
Scotland, Argyll, Glen Crow, Beinn an Lochain, 600m. NN219075 (McAllister 17.4.1971), v.c.98
Scotland, Argyll, Cowal, Ben More, 690m. NS106907 (3 plants) (McAllister 7.8.1970), v.c.98
Scotland, Argyll, Tighnabruaich, Ardlamont, 15m. NR988642 (McAllister 10.4.1971), v.c.98
Scotland, Argyll, Tighnabruaich, 15m. NR986736 (McAllister 1980), v.c.98
Scotland, Argyll, Kilfinnan, 10m. NR93-79- (McAllister 8.1974), v.c.98
Scotland, Argyll, Glendaruel. NS020901 (McAllister 13.4.1971), v.c.98
Scotland, Argyll, Glen Massan, Creag Tharsuinn. (McAllister), v.c.98
Scotland, Dunbartonshire, Inveruglas, Kenmore Wood. NN324083 (McAllister 1975), v.c.99
Scotland, Dunbartonshire, nr. Bowling, Glen Arbuck. NS456737 (McAllister 8.1974), v.c.99
Scotland, Dunbartonshire, Cardross. NS33-77- (A. Rutherford 1986), v.c.99
Scotland, Clyde Is., Bute, Balnakailly wood, 10m. NS022742 (McAllister 8.1996), v.c.100
Scotland, Clyde Is., Bute, Blackfarland Bay, NR994728 (McAllister 8.1984), v.c.100
Scotland, Clyde Is., Arran, Glen Loig NR957346 (R. Bell 1993), v.c.100
Scotland, Clyde Is., Arran, N of Doon. NR886303 (R. Bell 1993), v.c.100
Scotland, E. Ross, nr. Ledmore. NC29-09- (M. Birch 25.9.1987), v.c.106

Scotland, E. Sutherland, nr. Lairg, Falls of Shin NC57-05- (M. Birch 26.9.1987), v.c.107

**Viviparous tetraploid 2n=52 or *c*.52**

Wales, Carnaervon, Carnedd Dafydd, 750m. SH672633, 667633. (2 plants) (Q.Kay, McAllister), v.c.49
Wales, Carnaervon, Glyders, Cwm Idwal, 465m. SH6458 (McAllister 20.11.73), v.c.49
Wales, Carnaervon, Glyders, Devil's Kitchen, 660m. SH638588 (McAllister 22.11.1973), v.c.49
Wales, Carnaervon, Snowdon, Clogwyn y Garnedd, 1005m. SH611545 (McAllister 30.5.73), v.c.49
Wales, Carnaervon, Snowdon, Cwm Glas, 1005m. SH615554 (McAllister 10.2.1974), v.c.49
Wales, Carnaervon, Snowdon, Dinas Mot. SH625563 (McAllister 1974), v.c.49
England, Cumberland, Scafell Pikes, 600m. NY221081 (McAllister 8.10.1970), v.c.70
Scotland, Argyll, Arrochar, Ben Ime, 900m. (McAllister 23.9.1966), v.c.98
Scotland, Argyll, nr. Invereray, Beinn Bhuidhe. 900m. NN204186 (2 plants) (McAllister 5.10.1968), v.c.98

***Other localities confirmed morphologically from cultivated plants (some might be triploid)***

Scotland, W. Perth, Inverarnan, Ben Chabhair, 900m, NN366179 (McAllister 25.5.1968), v.c.87
Scotland, Argyll, Nr.Arrochar, The Cobbler, 780m, NN261058 (McAllister 25.9.1963), v.c.98
Scotland, Argyll, Ben Cruachan, 360-1100m, NN072306 (McAllister 5.8.1973), v.c.98
Scotland, Argyll, Ben Lui, 600m, NN262274 (McAllister 30.10.1966), v.c.98
Scotland, Argyll, Glen Orchy, Ben Udlaidh, 740m, NN27-33- (McAllister 5.8.1967), v.c.98
Scotland, Dunbartonshire, Ben Vorlich, 900m, NN29-12- (McAllister 6.8.1967), v.c.99

***Deschampsia parviflora***

England, N. Wiltshire, Savernake Forest, SU23-65- (2 plants) (McAllister 10.1986), v.c.7
England, East Sussex, Ardingley, Wakehurst Place. TQ3--3-- (McAllister 10.1996), v.c.14
England, Oxfordshire, Henley-on-Thames. SU7--8--, v.c.23
England, Bedford, Mosebury Park, TL0--5-- (McAllister 27.10.86), v.c.30
England, W. Gloucestershire, Tetbury Westonbirt arboretum, Silk Wood ST8--9-- (McAllister), v.c.34
Wales, Carnaervon, Bangor, Treborth, SH553712 (McAllister 2.1987), v.c.49
Wales, Flint, Loggerheads. SJ200627 (McAllister 1975), v.c.51
Wales, Flint, Ysceifiog, SJ14-71- (G. Wynne 1982), v.c.51
England, W. Lancashire, Wyre Forest, SD4--4-- (E. Greenwood 1987), v.c.60
England, NEYorkshire, Malton, Castle Howard. SE718703 (2 plants) (McAllister 11.1986), v.c.62
England, MW Yorkshire, Grassington, Grass Woods. 290m. SD984654 (McAllister 12.1974), v.c.64

England, MW Yorkshire, Wharfedale, Barden, SE052572 (2 plants) (McAllister 10.1986), v.c.64
England, MW. Yorkshire, Wharfedale, The Strid, SE07-55- (McAllister 10.1986), v.c.64
England, MW. Yorkshire, Wharfedale, Bolton Abbey, SE076542 (4 plants) (McAllister 10.1986), v.c.64
England, MW Yorkshire, Bingley, Eldwick, Beck Bottom, SE124704 (McAllister 10.1986), v.c.64
England, MW. Yorkshire, Shipley Glen. SE135387 (McAllister 10.1986), v.c.64
England, Co. Durham, Upper Teesdale, High Force, Sand between rocks below falls, NY882285 (McAllister 6.1987), v.c.66
Scotland, Ayr, NS355214. (4 plants) (McAllister 10.1986), v.c.75
Scotland, South Aberdeenshire, Seaton Park, rocks by River Don in woodland, NJ90 (McAllister 12.4.2007), v.c.92

***Deschampsia alpina* (2n=52) *x D. cespitosa* (2n=26)*.* 2n=39 (viviparous)**
Scotland, Westerness, Ben Alder plateau, NN482725 (McAllister 2.8.1970), v.c.97
Scotland, Westerness, Ben Alder, Garbh Coire, NN497716 (McAllister 2.8.1970), v.c.97
Scotland, Argyll, Glen Coe, Bidean nam Bian, NN142543 (McAllister 8.1974), v.c.98
Scotland, M Ebudes, Mull, Beinn nan Gabhar, NM543364 (McAllister 15.7.1968), v.c.103
Scotland, Outer Hebrides, South Uist, Beinn Mhor, NF81-31- (McAllister 5.1979), v.c.110

***Deschampsia cespitosa* (2n=52) *x D. cespitosa* (2n=26) 2n= 39 (viviparous)**
Scotland, Argyll, nr. Invereray, Beinn Bhuidhe. NN204186 (2 plants) (McAllister 5.10.1968), v.c.98
Scotland, Argyll, Cowal, Ben More. NS106907 (McAllister 8.1971), v.c.98