Ecology, distribution and fertility of *Carex recta* Boott (Cyperaceae) in the British Isles

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ABSTRACT

The rare sedge *Carex recta* is found on three estuaries in northeast Scotland. Field surveys and recording of associated species indicate that it thrives in different NVC. communities, ranging from mires, through tall-herb fen, rush pasture and mesotrophic grassland to salt-marsh. Seed fertility is low and varies between populations, with the highest fertility detected in the population along the River Wick where introgression occurs. The distribution is updated with one new population and the re-discovery of another.

KEYWORDS: *Carex recta*, Cyperaceae, ecology, NVC, fertility, Scotland.

INTRODUCTION

Carex recta Boott (Estuarine Sedge) is a perennial sedge with creeping rhizomatous growth. It has flowering stems up to 100 cm high and leaves up to 130 cm long and 4·0–7·5 mm wide. The upper 2–6 spikes (typically 3–4) of the inflorescence are male. The lower 2–6 spikes (typically 2–3) are female. Female spikes are from 20–80 mm long with peduncles up to 35 mm long on the lowest spike. The female glumes have an acute, acuminate or awned apex, with the lower glumes of the lower female spikes almost always awned. Awns are short, usually 1–3 mm long. *C. recta* has two stigmas, a biconvex utricle and a nut with a strong invagination. It is a boreal-montane, suboceanic hemicryptophyte (Hill *et al*. 2004) and is designated as vulnerable (JNCC 2009).

This sedge has been little studied in the British Isles since the work by John Faulkner (1972, 1973) who investigated cytology alongside intra- and inter- specific experimental crosses on *C. recta* and other species in section *Phacocystis*. Disturbed meiosis and low intraspecific fertility suggested that *C. recta* in Scotland was of hybrid origin (Faulkner 1972, 1973). Higher seed set from cross-breeding to both *C. aquatilis* Wahlenb. and *C. paleacea* Wahlenb. compared to the other section members implied that they were the probable parental species (Faulkner 1973), although only one of these parents, *C. aquatilis*, is recorded in the British Isles (Jermy *et al*. 2007). The same origin has been confirmed by karyology and isozymes in North America (Cayouette & Morisset 1986a, b; Standley 1990). The fertility of natural North American populations was assessed as good (Cayouette & Morisset 1985). The fertility of natural British populations has not previously been examined.

C. recta is recorded from only three estuaries in north-east Scotland (Wigginton 1999; Preston *et al*. 2002; Cheffings *et al*. 2005). The distribution of the sedge along each of these estuaries is different. The distribution given in an earlier study included only the briefest details of each site (Dean & Ashton 2006). More detailed accounts from fieldwork by MD are given here. In addition, recent work has discovered one new population and confirmed the presence of another population, thus updating the current distribution. A brief account of the ecology and associated species (Jermy *et al*. 2007) indicates that the sedge may be found in the S27 tall-herb fen community. However, this is an oversimplification and variation of the communities in which the species is found requires more detailed consideration. From surveys of the vegetation communities associated with the larger sedge stands a more comprehensive account is provided here.

The aims of this paper are therefore; to record associated species and determine the National Vegetation Classification (NVC.) plant communities associated with four large populations of *C. recta*, to record life history, to examine the fertility of *C. recta* and its backcross to *C. aquatilis* (*C.* × *grantii*) from percentage of seed set, and to update the distribution.

TABLE 1. SPECIMENS USED IN THE STUDY OF THE FERTILITY OF *CAREX RECTA* AND *C.* × *GRANTII* IN THE BRITISH ISLES

Taxon	No. of culms	Collection date	Location	Grid ref.	v.c.
C. recta	20	August 2002	Wick	ND354514	109
C. recta	20	September 2001	Beauly*	NH539465	96
C. recta	20	September 2001	Invershin*	NH578953	106
C. recta	20	September 2001	Bonar Bridge*	NH6091	106
C. × *grantii*	20	August 2002	Wick	ND358516	109

*specimens collected by C. B. Ballinger

METHODS

SURVEYS FOR RECORDING SPECIES ASSOCIATED WITH *C. RECTA* AND NVC PLANT COMMUNITIES

Four sites where *C. recta* is the dominant species were used in the vegetation study and were chosen because there is a large sedge stand present. *C. recta* is also found as a minor component of some communities but these were not surveyed. On the rivers Wick and Beauly the main stands are restricted to a relatively short length of river. Two sites, Invershin and Bonar Bridge, were chosen from the extensive range found on the Kyle of Sutherland/River Oykel. Bonar Bridge was split into west and east of the road bridge as the environmental conditions differ between the two close sites: the west side is relatively sheltered with river defence barriers and creeks, the east side is exposed. The species associated with *C. recta* were identified and recorded. MATCH (version 2.11) software from the Unit of Vegetation Science, University of Lancaster, was used to generate short lists of possible NVC communities from the species lists by site. These possible communities were examined against NVC descriptions to determine the most appropriate classification (Rodwell 1991a, 1991b, 1992, 1995, 2000). Distribution and life history details were also recorded during surveys.

FERTILITY

Culms from *C. recta* and *C.* × *grantii* were collected in August and September when nuts and utricles would have matured if they were fertile (Table 1). The utricles were removed then observed at 10× magnification under a microscope to determine whether they contained a mature nut. Many utricles were flattened and distorted in shape, and it was obvious that they did not contain a fertile nut. Only swollen utricles were tested for containing a potentially fertile nut, by squeezing the utricle between watchmaker's forceps. Filled, and therefore potentially fertile, nuts within the utricles did not yield to pressure, but non-viable nuts squashed under pressure. Preliminary work in the department (unpublished), comparing this method with staining of embryonic tissue with tetrazolium dye, had established that this was a valid approach. Utricles were counted into two groups, potentially fertile and infertile utricles per culm. Samples were compared by Analysis of Variance (ANOVA) followed by the Tukey test (used when ANOVA has detected that at least one of the sample means is significantly different, to work out where the differences lie).

RESULTS

LIFE HISTORY

The rhizomes and roots of *C. recta* form a dense, entangled mat just below the substrate surface. In *Carex* generally the initial stages of a new vegetative or flowering shoot are protected by the outer, short, tough leaves (see Figure 2 in Jermy *et al*. (2007)). These short leaves are covered by cuticular wax, giving a pale glaucous colouration, and the tip of the tightly closed shoots forms a sharp point. New shoots are initiated in late summer and become dormant around November (Smith 1966). During winter the overwintering new shoot is often showing above the substrate by 2–3 cm, whereas the sedge leaves from the previous summer and vegetation of the associated species die back leaving an area covered with the remains of the dead vegetation.

In early May, the appearance of the tidal flats and marshes inhabited by *C. recta* indicates that the sedges have been completely covered by high tides or high river levels during the autumn or winter. *C. recta* and spring-flowering species such as *Caltha palustris* are the first

species to show signs of new growth. The flowering shoots of *Carex recta* start to grow earlier than the vegetative shoots. By early to mid May, at the tips of the culms, the male spikes of some specimens of *C. recta* are visible, but the anthers have not yet dehisced. The male glumes have the purple-brown – black-brown colour seen in mature specimens. On a few specimens the uppermost female spike is just emerging from the middle of the culm leaves which sheath the lower part of the culm. The female spikes are very immature, the utricles pale green and the female glumes pale-green/whitish and almost translucent, with the central nerve pale green. In the first half of May, the tallest vegetative leaves are up to 50–55 cm high at Wick and Beauly, up to 35 cm at Invershin, and up to 30 cm at Bonar Bridge East. In some stands the glaucous cuticular wax has not been abraded from the leaf surface, giving a pale blue-grey coloured tip to the normal matt mid-green/yellow-green colouration. During the spring, the sedges are the tallest species in their habitats, and show a pattern of growth assumed to maximise wind pollination. During the spring, some of the stands appear to consist almost entirely of *C. recta.* However, no *C. recta* seedlings were seen at any of the sites during the course of the fieldwork.

By the middle of July, the *C. recta* leaves have developed and are higher than the culms. At Wick, Beauly and Invershin other tall species have grown and are flowering, for example *Deschampsia caespitosa*, *Phalaris arundinacea* and *Filipendula ulmaria* (Table 2.). The sedges appear as an intrinsic part of the community, and in some places they are no longer dominant. As the female spikes develop, the colour of the female glumes changes to the purple-brown – black-brown typical of section *Phacocystis* in the British Isles. The utricles remain green until they mature to a pale brown – hay-colour in August or September. In some years the *C. recta* at Beauly is sparse-flowering with very few flowering spikes to be found. The sedge flowers more freely at Wick, Invershin and Bonar Bridge.

FIELD SURVEYS

The results of field surveys between 1999 and 2004 were summarised in an earlier paper (Dean & Ashton 2006). Detailed site descriptions are given here, updated by surveys since 2004. On all three estuaries *C. recta* was found below the high water mark and at altitudes below 10 m (see Fig. 1).

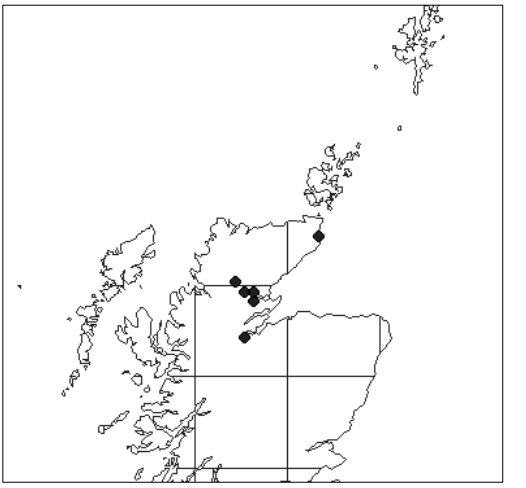

FIGURE 1. Distribution of *Carex recta* in Scotland in 10km squares

RIVER WICK (V.C.109)

The north bank of the River Wick, immediately west of Wick, is broad and flat, with a few shallow channels, and is generally marshy. Several freshwater ditches drain the surrounding farmland. *C. recta* is found in the marshy areas and across the full width of the estuarine flats, encroaching into the ends of the fields if they are marshy. In some stands *C. recta* forms a dense mass of vegetation, and is almost the only species present (ND354514). In other areas there are *C. recta* and apparent *C. recta* backcrosses to *C. aquatilis* scattered among tall riverbank vegetation and from July onwards the sedges may be difficult to find amongst the taller marsh vegetation. *C. aquatilis* is also present, and whereas *C. recta* is typically found in the flat, marshy areas of the river bank, where there is a gentle slope into the river, *C. aquatilis* is found at the very edge of the river and may form a linear stand less than 1 m wide on the top of the bank where there is a drop to the river. The main area of river estuary on which *C. recta* was found is approximately 500 m long on the north bank. Sedge stands were found up to approximately 1 km further upriver, but these are mainly *C. aquatilis* or *C.* × *grantii*.

TABLE 2. SPECIES ASSOCIATED WITH *CAREX RECTA* IN THE BRITISH ISLES

Species	Wick	Beauly	Inversh in	Bonar Bridge[1]		No. of locations	Estuarine species[2]
				East	West		
Achillia ptarmica			+			1	
Agrostis stolonifera	**+**	**+**	**+**	**+**	**+**	**5**	
Alnus glutinosa			+			1	
Alopecurus geniculatus		+		**+**	**+**	3	
Armeria maritima				+		1	×
Anemone nemorosa			+			1	
Angelica sylvestris	+					1	
Anthoxanthum odoratum					+	1	
Aster tripolium		+	+			2	×
Aster × *salignus*		+				1	
Atriplex glabriuscula	+					1	×
Bolboschoenus maritimus				+		1	×
Callitriche stagnalis				**+**	**+**	2	
Caltha palustris	**+**	**+**	**+**		**+**	4	
Calystegia sepium			+			1	
Cardamine pratensis		+	+	+		3	
Carex aquatilis	+					1	
Carex nigra			+			1	
Carex rostrata			+			1	
Centaurea nigra	+					1	
Cerastium fontanum				**+**	**+**	2	
Chamerion angustifolium			+			1	
Cochlearia anglica				+		1	×
Cochlearia officinalis	+	+		+	+	4	×
Crepis capillaris				+		1	
Crepis paludosa			+			1	
Cynosurus cristatus					+	1	
Deschampsia cespitosa		+	+			2	
Deschampsia flexuosa		+		+		2	
Eleocharis palustris			+			1	
Eleocharis uniglumis				**+**	**+**	2	
Elytrigia repens	+					1	×
Epilobium palustre		+	+			2	
Equisetum fluviatile	+	+	+			3	
Equisetum palustre	+	+	+			3	
Filipendula ulmaria	+	+	+			3	
Festuca arundinacea				+		1	
Festuca rubra		+		**+**	**+**	3	×
Galium aparine	+	+	+			3	
Galium palustre		+	+		+	3	
Glaux maritima				+		1	×
Heracleum sphondylium		+				1	
Holcus lanatus	**+**	**+**	**+**	**+**	**+**	**5**	
Holcus mollis	+		+			2	
Hydrocotyle vulgaris		+				1	
Iris pseudacorus	+					1	
Juncus articulatus	+	+			+	3	
Juncus bufonius					+	1	×

TABLE 2. CONTINUED

Species	Wick	Beauly	Invershin	Bonar Bridge[1]		No. of locations	Estuarine species[2]
				East	West		
Juncus effusus		+	+	**+**	**+**	4	
Juncus gerardii				**+**	**+**	2	×
Littorella uniflora			+			1	×
Lolium perenne					+	1	
Lotus pedunculatus		+				1	
Lythrum salicaria		+				1	
Mentha aquatica	+		+			2	
Menyanthes trifoliata			+			1	
Montia fontana				+		1	
Myosotis scorpioides	+	+	+			3	
Oenanthe crocata		+				1	
Pedicularis palustris			+			1	
Phalaris arundinacea	+	+	+			3	
Phragmites australis	+	+				2	×
Plantago lanceolata			+			1	
Plantago maritima	+			+		2	×
Poa humilis					+	1	
Potentilla palustris			+			1	
Ranunculus ficaria	+	+	+			3	
Ranunculus flammula		+	+	**+**	**+**	4	
Ranunculus repens			+			1	
Rumex acetosa		+				1	
Rumex acetosella		+	+			2	
Rumex crispus	+			+		2	×
Rumex obtusifolius	+	+				2	
Sagina procumbens				+		1	
Salix sp.			+			1	
Schoenoplectus lacustris	+					1	
Scutellaria galericulata			+			1	
Senecio jacobaea		+				1	
Stachys palustris	+					1	
Stellaria graminea		+	+			2	
Succisa pratensis		+				1	
Taraxacum officinale agg.				+		1	
Trifolium repens				**+**	**+**	2	
Triglochin palustre					+	1	×
Triglochin maritimum	+			**+**	**+**	3	×
Typha latifolia	+	+	+			3	
Valeriana officinalis	+	+	+			3	
Viola palustris			+			1	
Column total	29	37	41	26	22		17
				Bonar Bridge			
Location total	29	37	41	35			

Total number of species = 88
The two species found at all five locations are shown in **bold**
[1]Bonar Bridge separated into East and West of roadbridge due to differences in habitat
[2]habitat description in Stace (1997) includes estuaries, salt-marshes or brackish habitat

RIVER BEAULY (V.C.96)

From the town of Beauly eastwards along the north bank of River Beauly there is a high river defence bank, and the flat area of the bank next to the river is narrow, only a few metres wide. Approximately 1 km east of Beauly the river bends sharply northwards, the flat area widens, and a mudbank has formed in the river and is now a small, narrow, vegetated island. At this point there is one large stand on the flat area of the north bank (NH539465). Between *C. recta* and the muddy river edge there is a very narrow strip of *Juncus effusus*, then on the mud *Callitriche* sp. In the lagoon immediately north-east of the large *C. recta* stand there are several small patches of *C. recta* amongst the dominant *Phragmites australis*. On the north bank the *C. recta* was found within a length of 200–300 m. A population recorded on the south bank at Lentran Point had not been detected until a very small population was re-found amongst the *P. australis* in 2007 at NH584459 by C. B. Ballinger. These populations are within the Moray Firth SSSI.

KYLE OF SUTHERLAND/RIVER OYKEL (V.CS. 106,107)

The total length of river estuary on which *C. recta* is found is approximately 17 km with large populations at two separated sites. In places the sides of the river are steep and unsuitable for *C. recta*. Part of the area is within the Kyle of Sutherland Marshes SSSI. Furthest upriver is the population near Ochtow (NC486001) discovered in 2006 by C. B. and B. R. Ballinger. Furthest downriver are the populations on the north bank at Bonar Bridge (NH610914) and on the south bank at Kincardine (NH607894). Large populations can be found on both sides of the river near Invershin and on the south bank at Bonar Bridge. On the southwest bank below Carbisdale Castle there are stands of *C. recta* in a marshy area (NH578953) and around a small promontory (NH573958). On the opposite bank, near Invershin, the river widens as this bank curves away into a wide bay with a gently sloping bank. There is a narrow strip of *C. recta* all along the bank and in marshy areas. Some of the sedges on the north bank have the appearance of *C. recta* hybrids with *C. nigra* (*C.* × *spiculosa* Fries) and *C. nigra* is present. On the south-west bank at Bonar Bridge west of the bridge there are several small *C. recta* stands on the sides of the creeks (NH607917). In contrast to the east of the bridge there is a very large *C. recta* stand, approximately 95 m long by 75 m wide, situated where the south bank turns sharply south-west and the estuary widens (NH608913).

ASSOCIATED SPECIES AND NVC PLANT COMMUNITIES OF *CAREX RECTA* POPULATIONS

The associated species list shows that 88 associated species were recorded, 50 of them from one location only, and only two species, *Agrostis stolonifera* and *Holcus lanatus* recorded from all five locations (Table 2). Although *Carex recta* is found within the tidal range of estuaries and therefore is tolerant of at least low levels of salinity, only 17 of the associated species are noted as maritime or brackish habitat species in the British Flora (Stace 1997). Of these, ten were recorded from Bonar Bridge East. One additional associated species, a near threatened species in Britain, *Pilularia globulifera* (JNCC 2009), was found near Kilmachalmack (NH5099).

The associated species list for each location generated several possible NVC communities for each site. Following this process NVC communities for the five sites were analysed using familiarity with the dominant species within each community gained from the surveys and the community details given by Rodwell (1991a, 1991b, 1992, 1995, 2000). Wick was the most complex to resolve and the most appropriate NVC was M27a *Filipendula ulmaria-Angelica sylvestris* mire, though it might have elements of M22 *Juncus subnodulosus-Cirsium palustre* fen-meadow, OV26c *Epilobium hirsutum* community *Filipendula ulmaria-Angelica sylvestris* sub-community and S25 *Phragmites australis-Eupatorium cannabinum* tall-herb fen (Table 3.). The NVC for Beauly was straightforward and was identified as a mire community M23b *Juncus effusus-Galium palustre* rush pasture. The highest number of associated species was found at Invershin (Table 2), for which two communities were ranked similarly by the MATCH software, S27a *Carex rostrata-Potentilla palustris* tall-herb fen and W3 *Salix pentandra-Carex rostrata* woodland. The S27a community was selected for two reasons: many of the herbs recorded from this community are components of the S27a tall-herb fen, and the *C. recta* population lies in the zone between *C. rostrata* in the edge of the river and the woodland behind and the S27 community is considered typical of this transition zone (Rodwell 1995).

The two populations at Bonar Bridge are at more exposed sites, and have NVC communities that are different from each other and from the other three sites. At Bonar Bridge West, upriver of the roadbridge, small stands of *C. recta* are dominant, mainly at the edges of creeks but

TABLE 3. NATIONAL VEGETATION CLASSIFICATION (NVC) COMMUNITIES ASSOCIATED WITH *CAREX RECTA* IN THE BRITISH ISLES

Location	NVC	NVC community	NVC sub-community
Wick	M27a	*Filipendula ulmaria - Angelica sylvestris*	*Valeriana officinalis - Rumex acetosa*
Beauly	M23b	*Juncus effusus - Galium palustre*	*Juncus effusus*
Invershin	S27a	*Carex rostrata - Potentilla palustris*	*Carex rostrata - Equisetum fluviatile*
Bonar Bridge West	MG8	*Cynosurus cristatus - Caltha palustris*	-
Bonar Bridge East	SM16c	*Festuca rubra*	*Festuca rubra - Glaux maritima*

TABLE 4. SEED SET FOR *CAREX RECTA* POPULATIONS IN THE BRITISH ISLES

Location (no. of specimens)	Wick (20)	Beauly (20)	Invershin (20)	Bonar Bridge (20)
Fertility details per specimen				
Number of mature utricles (mean±sd)	16·1 ± 11·5 a	2·0[1] b	0·0[1] b	4·9 ± 3·9 b
range	0–37	0–13	0–7	0–14
Total number of utricles (mean±sd)	555·8 ± 89·0 a	422.6 ± 98.6 b	552.6 ± 138.1 a	330.7 ± 110.0 c
range	411–716	245–580	329–753	169–634
Percentage fertile (mean±sd)	2·8 ± 1·8 a	0·4[1] b	0·0[1] b	1·5 ± 1·1 c
range	0·0–6·3	0·0–2·7	0·0–1·3	0·0–3·7
Total female spikes length/mm (mean±sd)	156·7 ± 26·9 a	128·4 ± 27·8 b	170·4 ± 33·4 a	101·0 ± 20·2 c
range	103–199	86–169	107–226	73–148
Mean density of utricles per mm of female spike	3·5	3·3	3·2	3·3

[1]median shown if sd > mean
Variables followed by the same letter are not significantly different at $P = 0{\cdot}05$

also encroaching on grazed meadows. The sedges are the tallest species due to the preferential grazing of the surrounding turf which is kept short (Table 2). The meadow community is an MG8 *Cynosurus cristatus – Caltha palustris* mesotrophic grassland (Table 3). At Bonar Bridge East the sedges dominate the habitat and other species are infrequent. However, as *C. recta* has not been used in the determination of any NVC community, the community was determined by the other species present and was determined as SM16c *Festuca rubra* salt-marsh.

FERTILITY OF *CAREX RECTA* IN THE BRITISH ISLES

The number of filled utricles detected (the number of seed set) for *C. recta* ranged from 0 to a maximum of 37 per specimen at Wick (Table 4). Because the total number of utricles was high, the percentage seed set was very low at all locations, ranging from 0–6·3%. Wick had a significantly higher average number of mature utricles and fertility rate (percentage fertile) than the other three sites. Both Beauly and Invershin had a significantly lower fertility rate than the other two sites. Although there were significant differences in total number of utricles and the total length of female spikes, these two variables varied proportionately. This is reflected in the mean density of utricles per mm of female spike, an indicator of how tightly the utricles are packed on the female spikes, which varied little, ranging from 3·2 (Invershin) to 3·5 (Wick) (Table 4). There were significant differences between the two sites on the same river system, Invershin and Bonar Bridge, for total number of utricles, percentage fertile and total female spikes length. The sample from Wick of *C.* × *grantii* had higher means than the sample of *C. recta* from Wick for all variables. Only the total number of utricles per specimen was significantly higher (Table 5) indicating that the utricles are more densely packed on the *C.* × *grantii* female spikes.

TABLE 5. SEED SET AT WICK: *CAREX RECTA* COMPARED TO *C.* × *GRANTII* (BACKCROSSES TO *C. AQUATILIS*)

Taxon	*Carex recta*	*C.* × *grantii*
Location (specimens)	Wick (20)	Wick (20)
Fertility details per specimen		
Number of mature utricles (mean ± sd)	16·1 ± 11·5 a	25·3 ± 17·8 a
range	0–37	3–65
Total number of utricles (mean ± sd)	555·8 ± 89·0 a	663·6 ± 108·1 b
range	411–716	452–834
Percentage fertile (mean ± sd)	2·8 ± 1·8 a	3·6 ± 2·3 a
range	0·0–6·3	0·6–9·4
Total female spikes length /mm (mean ± sd)	156·7 ± 26·9 a	158·8 ± 21·9 a
range	103–199	105–189
Mean density of utricles per mm of female spike	3·5	4·2

Variables followed by the same letter are not significantly different at $P = 0{\cdot}05$

DISCUSSION

NVC DIFFERENCES BETWEEN SITES

Although *C. recta* is typically found in estuarine marshes and mud flats where there is a gentle slope from marsh to river, a different NVC community was determined for each of the five sites and included diverse habitat types including mires, tall-herb fen and saltmarsh. These differences may be attributed to recent history of the site, current use and local topography. Three locations, Wick, Beauly and Invershin are mire or fen type habitats, with tall herbs dominant (Rodwell 1991b, 1995). The River Wick has wide estuarine flats, dissected by run off ditches from grazed pasture, and is probably a complex of more than one habitat and community. Invershin has narrower flats and is situated below woodland. The River Beauly NVC is M23b *Juncus effusus – Galium palustre* rush pasture, and perhaps reflects recent history as it is below grazing land, and may have been the edge of such pasture before the high river defence was built. Bonar Bridge West is currently grazed and some grasses were found only on this site, for example *Anthoxanthum odoratum, Cynosurus cristatus,* and *Lolium perenne*. The MG8 community is characteristic of periodic inundation, which occurs here, and is considered the natural community of a traditional water meadow (Rodwell 1992). However, despite the other species being grazed, *Carex recta* is limited to the creek edges and spreads only sparsely into the edges of the meadow, indicating that it is outcompeted in that habitat, and is only a very minor constituent of the MG8 grassland. At Bonar Bridge East, where other species are scarce, *C. recta* is particularly dominant and the community was assessed as a *Festuca rubra* saltmarsh, which is the most likely community for the surrounding saltmarsh.

REPRODUCTIVE DIFFERENCES BETWEEN SITES

The intraspecific differences in fertility showed that seed set in *C. recta* was low, and, excluding Wick where backcrossing may have occurred, the highest mean seed set was 1·5% at Bonar Bridge. This supports findings of similar low seed set from experimental intra-specific crosses, in which mean seed set was 1·9% (Faulkner 1973). The highest percentage of filled utricles came from Wick, the only British location where the parental species *C. aquatilis* is present. Generally, amongst plant hybrids, because most F_1s are only partially fertile at best, most of the effective fertilizations in which a hybrid takes part will involve one of its parents as the other partner (Grant 1971). Therefore it is suggested that some of the pollinations were by *C. aquatilis*, and this has increased the fertility rate. A sample of *C.* × *grantii* from Wick had slightly higher fertility than *C. recta* from Wick, indicating that backcrossing to *C. aquatilis* increased fertility, but not significantly. No attempt has been made to germinate seed, but North American *C. recta* seeds are viable (Standley 1990). Bonar Bridge had the second highest fertility, and this may be further evidence that the habitat at Bonar Bridge East, despite being more severe, is beneficial to *C. recta* due to lack of competition.

HABITAT RESTRICTIONS WITHIN RIVER SYSTEMS

C. recta populations appear to be restricted to three estuaries and there appear to be limited opportunities for it to extend its range within these estuaries. On two estuaries, Rivers Wick and Beauly, there is little or no opportunity for *C. recta* to migrate to more ecologically favourable habitats. Although the River Wick has a large marshy habitat on the north bank, which currently supports a large population, downriver the river is canalised through the town centre, then opens into two harbours. The estuary sides and coastline east of Wick are rocky and unsuitable for *C. recta*.

River Beauly has the smallest population, one very small population on the south bank, one large stand on the north bank, and a few scattered sedges in one lagoon. Beauly has several similar lagoons, but the others are dominated by tall vegetation, mainly *Phragmites australis* and *Typha latifolia* and no *C. recta* was found there during surveys. Parts of the south bank opposite these populations are marshy and inaccessible, but are likely to be suitable habitats for *C. recta* and the sedge may be extant there. The north bank population has been recorded as reduced in size since the 1980s (Wigginton 1999; Preston *et al*. 2002). This population may be the one most at risk from localised changes. The habitat at Beauly is situated below a high river defence bank with the large sedge stand located on the flat riverbank, covering the width of the bank, opposite a small estuary island. The sedges are bordered by tall vegetation at both ends on the flat. The population appears unable to expand, and is more likely to contract. A narrow channel runs between the bank and the island. Estuary coastlines and estuary islands are relatively temporary, affected by, for example, water circulation, tidal circulation, sedimentation processes and human impact (Day *et al*. 1989). In the longer term, although there is a long estuary downriver of Beauly, ordnance survey maps indicate mainly shingle or sand on the narrow estuarine flats, backed by manmade features, such as roads. There do not appear to be suitable habitats for migration.

By comparison the Kyle of Sutherland has several medium to large populations. It is not known if these populations are contemporaneous in origin, or if downriver (or possibly upriver) populations are of a later origin resulting from detached clumps or floated seed. There are several, small, satellite populations downriver from Bonar Bridge, and this suggests that *C. recta* has successfully migrated downriver on the Kyle of Sutherland. However, no genetic work has been carried out to date to identify if there are genetic similarities between populations. The banks of the Kyle further downriver show a similar lack of potentially habitable sites as it also has roads close to the shoreline.

Although the surveys have been extensive, there are areas where access is difficult that have not been surveyed. Some fieldwork was undertaken at Loch Fleet, a large site with a long shoreline, from where the sedge has been recorded (Anthony 1976). In many parts the habitat does not appear correct for *C. recta* and surveys of other parts did not shown any trace of the sedge. Between the river systems of the Kyle of Sutherland and River Beauly populations, there is the Cromarty Firth which was surveyed briefly along the north bank downriver from Dingwall, but there was no trace of the species.

NATURAL PROPAGATION OF *CAREX RECTA*

Although *C. recta* produces a small amount of potentially fertile seed, from observations, it reproduces entirely vegetatively. However, sexual reproduction and seedling recruitment cannot be ruled out and this is most likely along the Kyle of Sutherland, where populations are found on exposed estuary flats with adjoining areas of bare mud. Absence of seedlings does not necessarily mean the population is genetically uniform, because lack of seedling recruitment has been reported for *Carex* populations that have been genetically diverse, indicating that sexual reproduction has occurred in the past (McClintock & Waterway 1994; Jonsson *et al*. 1996; French *et al*. 2005). However, new genes allowing adaptations may arrive from related species by introgression, for example the introgression from *C. aquatilis* into the River Wick population leading to increased fertility. Such local introgression may also support the suggestion of genetic variation between populations and supports the possibility of sexual reproduction. Further support for genetic variation between populations comes from the intraspecific macro- and micromorphological variation detected (Dean, 2006). Although there is little scope for further spread in its current locations, variation between populations resulting from introgression or hybridisation with close relatives may be occurring, leading to local adaptation following natural selection.

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