A reassessment of the distribution of *Carex recta* Boott (Cyperaceae) in the British Isles

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ABSTRACT

Carex recta Boott (Cyperaceae), Estuarine Sedge, is a rare sedge in the British Isles and is currently known from only three sites in Scotland. At another Scottish locality a presumed hybrid *C. acuta* × *recta* has been identified. The morphological distinction between *C. recta* and *C. acuta* was investigated using qualitative and quantitative characters. Using the characters that discriminate between these two species, the presumed hybrid has been reassessed and is identified as *C. recta*.

KEYWORDS: Estuarine Sedge, hybridisation, morphology, multivariate analysis.

INTRODUCTION

Carex recta Boott (Estuarine Sedge) is one of the seven species in *Carex*, subgenus *Carex*, section *Phacocystis* found in the British Isles. It is a Red Data Book species currently recognised from only three 10 km squares, all located in north-eastern Scotland (Wigginton 1999; Preston *et al.* 2002). *C. recta* grows in brackish marshes and on the tidal flats of rivers and estuaries, towards the upper parts of the tidal influence. It is found where there is a supply of fresh water draining into the area. Although a rare sedge in the British Isles, it has an amphiatlantic distribution and is not uncommon in parts of its North American range where it extends from the shores of Hudson Bay and along the coast and river estuaries on the eastern coast from Labrador in the north to Maine in the south (Cayouette & Catling 1992).

The earliest records of *C. recta* in the British Isles are from specimens collected as *C. kattegatensis* Fr. and *C. salina* var. *kattegatensis* Almq. from the River Wick in 1885 by J. Grant and H. N. Ridley (Marren 1999). It was subsequently found and collected from the River Beauly in 1888 by G. C. Druce, and in 1967 Faulkner discovered the third site on both banks of the Kyle of Sutherland at Invershin. Downriver from the location at Invershin, close to Bonar Bridge, are several stands of sedges with the characteristics of species in section *Phacocystis*. The local Flora records carices at Bonar Bridge as representing another member of the section, *C. acuta* L. (Slender Tufted Sedge) "det. Chater with signs of introgression with *C. recta*" (Duncan 1980).

Specimens in this section presenting the typical morphological form can be separated using any of the sedge keys to British species, for example (Jermy *et al*. 1982; Rose 1989; Sell & Murrell 1996; Stace 1997). However, due to intraspecific morphological variation, hybridisation and introgression, this section has been considered difficult, and uncertainty over the correct identification of some specimens is recognised across Europe (Sylvén 1963; Hylander 1966; Jermy *et al*. 1982). In the field the Bonar Bridge populations present many similarities to *C. recta*. Although all the specimens examined had long female glumes at the base of the female spikes, not all of them had awned glumes in this position, the feature often considered characteristic of *C. recta*.

As there are so few sites for this species it is important to establish its current distribution. This paper aims to reassess the identification of the Bonar Bridge populations, currently reported as *C. acuta* × *recta*, using morphological and stomatal density measurements. Multiple characters have been analysed in recent studies to determine relationships between closely related *Carex* taxa (Blackstock & Ashton 2001; Řepka 2003). Similar techniques may also reveal novel character combinations that are useful in distinguishing between these taxa.

METHODS

Live material of *C. recta*, *C. acuta* and the Bonar Bridge carices was examined for this study (Table 1). Herbarium material (**OXF**) was used to supplement measurements made in

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TABLE 1. ORIGINS OF *CAREX* SECTION *PHACOCYSTIS* SPECIMENS USED IN THE STUDY

Taxon	Location	Grid Ref.	v.c.	No. of specimens used: Morphological study	No. of specimens used: Stomatal density
C. recta	Wick, north bank River Wick, Caithness	ND354514	109	22	10
	Invershin (south bank), E. Ross	NH578953	106	21	10
	River Beauly, Beauly, Easterness	NH539465	96	19	10
C. acuta	Formby, Merseyside	SD278071	59	10	1
	Lazonby, Cumbria	NY552403	70	5	1
	Edenhall, Cumbria	NY571327	70	3	1
	River Severn, Shropshire	SJ538085	40	1	1
	Three Cornered Meadow, Denbighshire	SJ406582	50	1	6
Bonar Bridge taxon	Bonar Bridge West of road bridge, E. Ross	NH607917	106	19	5
	Bonar Bridge East of road bridge, E. Ross	NH608913	106	20	5

the field. Stomatal density data were obtained from plants in cultivation.

The total of 62 characters that were used in this study were separated into quantitative and qualitative characters, and specimens were measured and assessed in the field in June and July 2001 and July 2002. Characters examined for this study were selected from the characters used for section *Phacocystis* by Standley (1987) with additional characters considered relevant to *C. recta* and *C. acuta*. Morphometric measurements were made in the field from randomly selected culms and vegetative shoots from specimens at least 2 m apart. Wherever possible, culms and vegetative shoots were taken from the same genet, although in some cases the closely packed nature of the stands of sedges means it was not possible for this to be determined. Measurements of the youngest mature leaf (i.e. the one most central to the vegetative shoot or flowering shoot) were recorded separately for vegetative leaves, defined as the leaves forming a sterile shoot, and for culm leaves, defined as the leaves surrounding the basal part of the culm and forming a fertile shoot. In a few specimens the culm leaf was sheathing the culm for just over half its length, so in these specimens culm leaf width was measured from 1 cm above the top of the sheath instead of at the midpoint.

Due to lack of fertility and mechanical damage, there were incomplete data for some specimens. To maintain consistency of characters employed in the analysis with minimum loss of data, these characters were excluded. This meant that the qualitative characters often used to distinguish between species such as female glume and utricle characteristics were not available for use (Jermy *et al*. 1982). The 17 qualitative and 14 quantitative characters used in further analysis are shown in Table 2. Quantitative analyses of genus *Carex* have used similar numbers of characters: eleven characters (Blackstock & Ashton 2001), 15 characters (Waterway 1994), 17 characters (McClintock & Waterway 1994) and 27 characters (Řepka 2003).

Qualitative characters were checked for consistency within a taxon and compared for differentiation between taxa. MINITAB™ version 13 software (Minitab Inc. 2001) was used to calculate analysis of variance (ANOVA), principal components analysis (PCA) and discriminant analysis (DA). Prior to running ANOVA, quantitative data were checked for normality and outliers using Anderson-Darling test and boxplots respectively. Variances were checked manually as automatic testing of variance can be too sensitive (Quinn & Keough 2002). Log_{10} and square root transformations were used to reduce deviations from normality, and where this did not remove outliers, ANOVA was run both with and without outliers. Following ANOVA testing, characters for which there was a significant difference at the 5% level were further analysed by Tukey's HSD test. Standardised scores with a mean of zero and standard deviation of one were used for PCA,

TABLE 2. MORPHOLOGICAL CHARACTERS ANALYSED

	Quantitative characters		Qualitative characters
1	Proximal bract length	1	Auricles at bract base - absent/present
2	Proximal bract width at midpoint *	2	Culm angle shape - obtuse/acute
3	Culm leaf length*	3	Culm angle texture - smooth/rough
4	Culm leaf width at midpoint*	4	Culm leaf margin teeth - absent/present
5	Culm length*	5	Leaf (vegetative) margin teeth - absent/present
6	Inflorescence length	6	Leaf (vegetative) section type - v-shape/keeled/ plicate
7	Leaf (vegetative) length	7	Leaf (vegetative) tip shape - trigonous/not trigonous
8	Leaf (vegetative) width at midpoint	8	Leaf sheath mouth shape - concave/straight/convex/ diagonal
9	Ligule length	9	Leaf sheath on decaying - persists entire/becomes fibrillose
10	Female spike length (distal female spike)*	10	Ligule (vegetative leaf) apex shape - acute/obtuse/ rounded
11	Peduncle length (distal female spike)*	11	Ligule length (relative to leaf width) - >leaf width/ <= leaf width
12	Female spike length (proximal female spike)	12	Female glume colour
13	Peduncle length (proximal female spike)*	13	Female spike (distal) orientation - erect/pendent
14	Male spike length (terminal spike)*	14	Female spike (distal) male at apex - absent/present
		15	Female spike (proximal) orientation - erect/pendent
		16	Utricle beak - indistinct/distinct short-beak
		17	Utricle nerves - absent/present

* indicates 8 characters used in second DA

which was run using a correlation matrix. DA processed two *a priori* groups of *C. recta* and *C. acuta* using linear discriminant analysis. The sample of the taxon from Bonar Bridge was then added to the DA to predict group membership. The two original groups are not of equal size (62 and 20) and the larger group can have undue influence (Hair *et al*. 1998). A second DA was run with a randomly selected subset of the *C. recta* sample containing 20 specimens so that both groups were the same size. It is recognised that this is a small total sample size for DA, and it necessitated reducing the number of variables from 14 to eight to maintain the 5:1 ratio of specimens to variables recommended (Hair *et al*. 1998). Variables retained were those for which ANOVA had calculated the greatest significant differences in means between the *C. recta* and *C. acuta* samples.

Specimens for the stomatal density study were selected from those in cultivation at Edge Hill, with one mature leaf per specimen used (Table 1). Epidermal replicas of both leaf surfaces were obtained from the middle 5 cm of mature vegetative leaves and applied to microscope slides, adapting a method used for the leaves of grasses (Poaceae) (Rice *et al*. 1979). Stomata were counted from near the central vascular bundle of the leaf in a quadrat formed by a square graticule using 400× magnification. Five replicates per surface were counted per specimen, and counts were converted to density/mm^2.

It is intended that voucher specimens will be deposited at Liverpool Museum (**LIV**) at the end of the associated work.

RESULTS

MORPHOLOGY

Eleven of the 17 qualitative traits considered are shared by *C. recta* and *C. acuta*, four do not present consistent traits and only two can be used to differentiate between the two species (Table 3). This lack of variation precluded any meaningful form of multivariate analysis of the qualitative data. The two are angle texture at the top of the culm (smooth in *C. recta* and rough in *C. acuta*), and absence/presence of nerves on the utricles (absent in *C. recta* and present in *C. acuta*). Comparing the traits presented by the Bonar Bridge sample for these

TABLE 3. *CAREX RECTA*, *CAREX ACUTA* AND BONAR BRIDGE TAXON QUALITATIVE CHARACTER TRAITS

No.	Character	*C. recta* trait	%	*C. acuta* trait	%	*C. recta* & *C. acuta* shared trait	Bonar Bridge taxon trait	%	alignment
1	auricles	present	94	present	100	yes	present	100	both
2	culm angle shape	acute	100	acute	100	yes	acute	100	both
3	**culm angle texture**	**smooth**	**90**	**rough**	**100**	**no**	**smooth**	**69**	**69% C. recta, 31% C. acuta**
4	culm leaf margin teeth	absent	74	absent	95	yes	absent	82	both
5	veg leaf margin teeth	absent	53	present	100	partial	absent	82	not as *C. acuta*
6	veg leaf section type	weakly plicate	66	weakly plicate	80	yes	weakly plicate	62	both
7	veg leaf tip shape	not trigonous	95	not trigonous	100	yes	not trigonous	100	both
8	leaf shth.mouth shape	concave	92	concave	65	yes	concave	100	both
9	leaf shth.on decaying	not fibrillose	100	not fibrillose	100	yes	not fibrillose	100	both
10	ligule apex shape	acute	97	acute	50	partial	acute	100	*C. recta*
11	ligule relative length	> leaf width	61	< or = leaf width	70	partial	> leaf width	72	*C. recta*
12	f glume colour	dark / black	100	dark / black	100	yes	dark / black	100	both
13	f sp. dist orientation	erect	97	erect	100	yes	erect	100	both
14	f sp. dist male apex	absent	53	present	85	inconclusive	absent	51	n/a
15	f sp. prox orientation	erect	87	erect	100	yes	erect	95	both
16	utricle beak	short-beaked	100	short-beaked	100	yes	short-beaked	100	both
17	**utricle nerves**	**absent**	**94**	**present**	**100**	**no**	**absent**	**100**	***C. recta***

The two characters that distinguish between the species are shown in bold
Characters and character traits are as shown in Table 2

TABLE 4. QUANTITATIVE CHARACTER MEANS (OUTLIERS INCLUDED) FOR *CAREX RECTA*, *CAREX ACUTA* AND BONAR BRIDGE TAXON

Character	*C. recta*	*C. acuta*	Bonar Bridge	*P*
Proximal bract length/mm	254 a	216 b	211 b	***
Proximal bract width at midpoint/mm	6·2 a	4·1 b	5·2 c	***
Culm leaf length/mm	538 a	738 b	507 a	***
Culm leaf width at midpoint/mm	6·7 a	5·3 b	5·5 b	***
Culm length/mm	728 a	1075 b	640 c	***
Inflorescence length/mm	181 ab	191 b	167 a	*
Leaf (vegetative) length/mm	1047 a	1243 b	1001 a	***
Leaf (vegetative) width at midpoint/mm	5·9 a	6·6 b	5·4 a	***
Ligule length/mm	6·5	5·7	6·5	ns
Female spike length/mm (distal female spike)	32·2 a	48·2 b	31·2 a	***
Peduncle length/mm (distal female spike)	4·5 a	0·4 b	5·3 a	***
Female spike length/mm (proximal female spike)	60	58	55	ns
Peduncle length/mm (proximal female spike)	14·2 a	3·6 b	20·0 c	***
Male spike length/mm (terminal spike)	30·0 a	45·5 b	26·5 c	***

P = level of significant difference: *<0·05; ** <0·01; *** <0·001. ns = no significant difference
Means followed by the same letter are not significantly different at *P* = 0·05
Means of characters transformed before ANOVA are shown as reverse of the transformation

two characters, utricles lack nerves, but culm angle texture was variable. The traits presented for three other characters, the absence of teeth on the vegetative leaf margin, acute ligule apex shape and ligule longer than leaf width, place the sample closer to *C. recta*.

ANOVA between the *C. recta* and *C. acuta* samples detected significant differences in means for eleven of the 14 characters. Removal of outliers from the data had no effect on the analysis as it did not change the level of significance of differences in means for any character. However, although the means may be significantly different, there is overlap in range between the samples in all 14 characters (data not presented). When the Bonar Bridge sample was included and the analysis included all three taxa, ANOVA detected significant differences in means between at least two taxa in twelve of the 14 characters (Table 4). In four of the twelve characters all three taxa were significantly different from each other. The Bonar Bridge sample has the lowest means for nine characters, the highest means for both peduncle lengths, and the same mean as *C. recta* for ligule length. *C. acuta* has the lowest means for both culm leaf width and bract width, the two characters for which the Bonar Bridge sample is intermediate (Table 4). Overall *C. acuta* is the tallest of the three and has the longest terminal male spikes and distal female spikes, *C. recta* is intermediate and Bonar Bridge the smallest. The range of measurements obtained from the Bonar Bridge sample also overlaps with the other two taxa for all characters. Removing outliers and rerunning ANOVA again had minimal effect on results.

The PCA of the three taxa involved, *C. recta*, *C. acuta* and Bonar Bridge, has not separated the taxa along any of the first three components, which contribute 30·6%, 20·6% and 11·9% of the variation respectively (Table 5). Characters contributing most to PC1 are culm leaf length, culm length and terminal male spike length, and to PC2 proximal bract width, culm leaf width and proximal female spike length. Graphically Figure 1 shows the extent of the overlap between these taxa on both PC1 and PC2. *C. acuta* does have the highest 13 scores along PC1, but does not separate along this axis because the remaining seven are within the range shown by the other two taxa. Bonar Bridge presents a similar range of scores to *C. recta* along both PC1 and PC2. All three taxa overlap along PC2 and PC3 (not shown), although the *C. acuta* scores cluster towards the higher end.

DA of the two *a priori* groups of the original *C. recta* and *C. acuta* samples correctly classified each specimen. The sample from Bonar Bridge was then added to the analysis for prediction of group membership and this assigned all 39 specimens to the *C. recta* group.

TABLE 5. LOADINGS FOR THE FIRST THREE PRINCIPAL COMPONENTS FROM PCA OF *CAREX RECTA*, *CAREX ACUTA* AND BONAR BRIDGE

Eigenvalue	4·2789	2·8826	1·6594
Proportion	0·306	0·206	0·119
Cumulative	0·306	0·512	0·630

Variable	PC1	PC2	PC3
proximal bract length	0·162	-0·297	**-0·533**
proximal bract width	-0·084	**-0·496**	-0·149
culm leaf length	**0·425**	0·068	-0·053
culm leaf width	0·030	**-0·472**	-0·127
culm length	**0·424**	0·057	0·147
inflorescence length	0·260	-0·292	-0·233
vegetative leaf length	0·324	0·142	-0·097
vegetative leaf width	0·262	-0·081	-0·037
ligule length	0·046	-0·013	-0·074
distal female spike length	0·274	-0·122	**0·524**
distal female spike peduncle length	-0·213	-0·288	**0·325**
proximal female spike length	0·128	**-0·384**	0·310
proximal female spike peduncle length	-0·253	-0·269	0·237
terminal male spike length	**0·401**	-0·067	0·223

The three highest loadings for each component are shown in bold

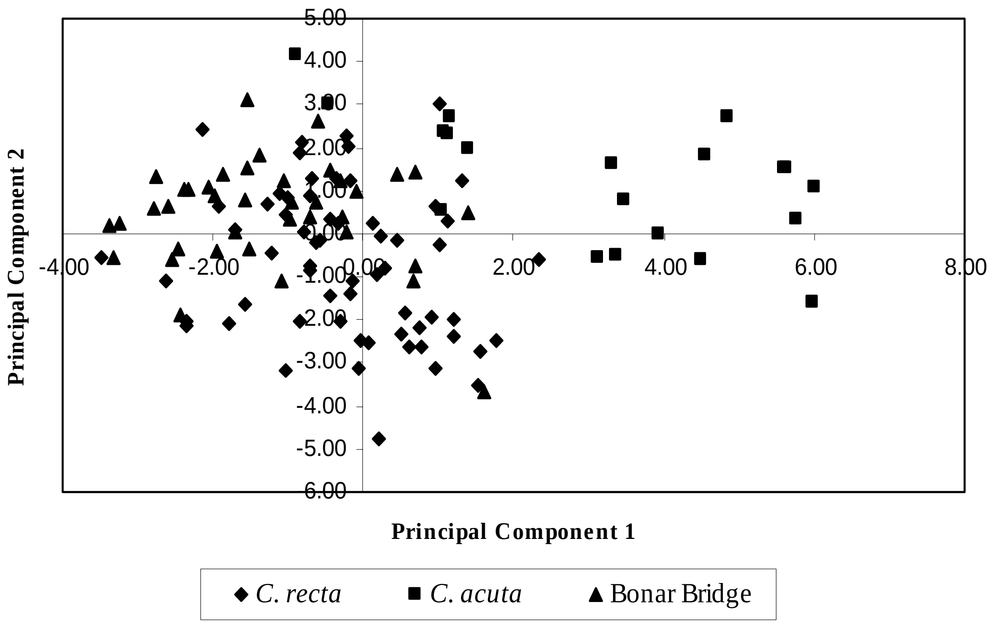

FIGURE 1. PCA Scatter Plot of PC1 v PC2 for *Carex recta*, *Carex acuta* and Bonar Bridge taxon.

TABLE 6. STOMATAL DENSITIES/MM²

	Adaxial surface			Abaxial surface		
Species/site	min	median	max	min	median	max
C. acuta	0	0	20	435	711	1225
C. recta Wick	0	20	138	178	365	573
C. recta Beauly	119	217	415	119	237	454
C. recta Invershin	138	375	474	79	237	415
Bonar Bridge taxon	79	277	494	59	217	454

For 35 specimens the probability that *C. recta* was the correct group was 100%, for the remaining four it was >90%. The second DA of the two even sized groups of 20 specimens and using eight characters also correctly classified each specimen as *C. recta* or *C. acuta*. The predicted classification for the Bonar Bridge specimens in the second DA was 38 *C. recta* and one *C. acuta*. 34 of the 38 are classified with 100% probability, and the remaining four with probability >95%. The one specimen classified as *C. acuta* was one classified as *C. recta* with <100% probability in the original analysis.

STOMATAL DISTRIBUTION AND DENSITY

There are differences in stomatal distribution between the *C. recta* samples. The Wick sample has no or few stomata on its adaxial surface whereas the other two samples are amphistomatous (Table 6). *C. acuta* has abaxial stomata and the abaxial stomatal density is much higher in this taxon than the other two taxa. The Bonar Bridge sample is amphistomatous and presents minimum, median and maximum densities that are similar to those of the *C. recta* samples from Beauly and Invershin.

DISCUSSION

Before the taxonomic position of the Bonar Bridge taxon can be addressed, the morphological characters that differentiate between *C. recta* and *C. acuta* need to be confirmed. Qualitative data showed that only two of the characters studied, smooth or rough culm angle texture at top of culm, and nerveless or nerved utricles, separated *C. recta* and *C. acuta* respectively (Table 3). To use just these two characters is insufficient, and is not completely reliable as some *C. recta* specimens had rough culm angles, so quantitative characters also need to be included. However, most of these show considerable overlap, even if the means are significantly different (Table 4). This emphasises the difficulties in working with morphologically variable taxa. It may not be possible to identify an individual specimen with certainty if it is not of typical form. Therefore it is beneficial to measure characters from sufficient specimens selected randomly from recognised populations to produce a table of character means, against which new specimens can be assessed. Considering the characters that may be useful in separating the two species, in general *C. recta* has shorter culms and culm leaves, shorter distal female spike and terminal male spike, and longer peduncles. In contrast, *C. acuta* is a larger sedge, with longer terminal male spike and distal female spike, but short peduncles, the distal female spike usually sessile. In addition, with sufficient specimens multivariate analyses can be used, and both the DA with the full *C. recta* sample and the DA with the equal sized *C. recta* and *C. acuta* samples classified all *C. recta* and *C. acuta* specimens correctly. This confirms that the set of characters used can differentiate between *C. recta* and *C. acuta*.

A hybrid taxon may be expected to be morphologically intermediate between the parental species in most characters (Flatberg 1972; Waterway 1994). However, an intermediate morphology is not found in the Bonar Bridge samples. Comparison with the differentiating criteria for qualitative characters, the Bonar Bridge sample usually has smooth culm angles and nerveless utricles, indicating an affinity with *C. recta* (Table 3). Analysis of quantitative characters (Table 4) indicates the Bonar Bridge samples generally have lower means than the other two taxa. Except for peduncle lengths, the Bonar Bridge sample is consistent with a smaller form of the *C. recta* found elsewhere in the British Isles. The sample means for several of the length characters, culm leaf, culm, inflorescence, vegetative leaf, distal female spike and terminal male spike, are significantly lower than the *C. acuta* sample, so the Bonar Bridge sample is much smaller than *C. acuta*. Overall, of the three taxa, the Bonar Bridge sedges are the smallest. Stomatal density and distribution also align the Bonar Bridge samples with *C. recta* (Table 6).

PCA did not separate the three taxa, but the complete overlap of the Bonar Bridge and *C. recta* samples along the first two axes implies a very close similarity between the two (Fig. 1). DA also identified a close proximity between *C. recta* and the Bonar Bridge taxon, classifying all 39 specimens as *C. recta* in the first run, and all but one in the second run with reduced volume of data.

There is also strong circumstantial evidence against the presence of a *C. acuta* × *recta* hybrid at Bonar Bridge. Although pre-1970 records indicate that *C. acuta* was found at Strathpeffer in the same vice county as the presumed hybrid (Duncan 1980), the current distribution of *C. acuta* in the UK extends no further north in Scotland than the Clyde-Forth line, so the recognised distributions of *C. acuta* and *C. recta* do not overlap (Preston *et al*. 2002). In addition studies including experimental hybridisation between *C. recta* and *C. acuta* produced a low mean seed set, although this was based on a small sample (Faulkner 1973). Combining these two observations it seems unlikely that this inter-specific cross would have occurred naturally.

The evidence presented from morphology, stomatal distribution and geographical location support the reassessment of the Bonar Bridge taxon as *C. recta*. This population and other small ones down river are new records for *C. recta* in East Ross-shire (v.c. 106). This increases the distribution of the plant in the UK from three to five 10-km squares. The *C. recta* population at Invershin, approximately 5 km upriver, is proposed as the progenitor of this population. Clumps detached from the main sedge stand at Invershin have been observed at the edge of the river, and could float downriver and be left stranded on the shoreline or on the edges of the creeks. It is proposed that such events led to the founding of the Bonar Bridge populations and the other small populations found along the estuary. The Bonar Bridge site to the east of the road bridge is very exposed, resulting in a smaller stature, and this may be a product of phenotypic plasticity.

CURRENT DISTRIBUTION

EASTERNESS V.C. 96

On the north bank of the River Beauly approximately 1 km east of the town of Beauly at NH539465. There is a large stand on the flat area beside the river and below the river defence bank. There are scattered sedges in the lagoon area just north of this at NH539466, but these become hidden by the tall, dense vegetation of *Phragmites australis* during the summer.

EAST ROSS-SHIRE V.C. 106

There are three locations on the south-western bank of the Kyle of Sutherland. Furthest upriver near Kilmachalmack from NH503990 to NH508989 although this stand is not continuous.

The second location is below Carbisdale Castle, where there are stands in marshy areas beside the river at NH573958, and there is a large stand of *C. recta* on the riverbank just upriver from the railway bridge at NH578953.

The third location starts at Bonar Bridge at NH6091. There are small stands to the west of the road bridge and one large population to the east of the road bridge. There are several small populations along the river's edge downriver as far as Kincardine including stands at the following grid references: NH604910, NH607894, NH607896 and the furthest downriver at NH605898.

EAST SUTHERLAND V.C. 107

There are locations on the north-eastern bank of the Kyle of Sutherland opposite those on the south-western bank in v.c. 106. Furthest upriver near Altass there is a stand on the riverbank at NH504992 and two stands in a marsh at NH503992 and NH505992.

At the second location near Invershin the population extends along the riverbank from NH575960 to NH578956. Some specimens show signs of hybridisation, probably with *C. nigra* (L.) Reichard. Small, scattered stands of *C. recta* are found upriver at the heads of small bays, for example at NH571967, NH570967 and NH570968. Only one small stand has been found at the third location, Bonar Bridge, at NH610914.

CAITHNESS V.C. 109

On both banks of the River Wick, but mainly on the north bank, just upriver from the town of Wick. On the north bank there is a large stand at ND354514. There are stands extending from ND354514 to ND350516, but amongst these there are stands with specimens that are introgressed or have hybridised with *C. aquatilis* Wahlenb. On the south bank the stands of *C. recta* show morphological characters of introgression to *C. aquatilis*. There is a stand at ND353513, and there are other small stands close by.

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