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Description, ecology and establishment of *Carex salina* Wahlenb. (Saltmarsh Sedge) – a new British species

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ABSTRACT

Carex salina (*Cyperaceae*) section *Phacocystis* is a species new to the British Isles, first discovered on a saltmarsh on the west coast of Scotland in 2004. Elsewhere it is found in the northern latitudes of western Europe and the north eastern seaboard of North America. The species is distinct from the closely related *C. recta* on the basis of habitat, distribution and morphology. It is also morphologically distinct from other closely related members of the same section. It is a component of saltmarshes similar in composition to those found elsewhere in its distribution. It has a hybrid origin, with neither parent recorded from the British Isles. It is most likely to have colonised following long distance dispersal, its establishment possibly facilitated by isostatic uplift (i.e. rise in land level due to relaxation of ice age conditions) and recent climatic changes.

KEYWORDS: Colonisation, Cyperaceae, hybridisation, saltmarsh, Scotland.

INTRODUCTION

The addition of a new species to the British flora is a rare event. Hence the discovery of a new *Carex* (Cyperaceae) species on the west coast of Scotland by one of the authors (KH) in July 2004 and the subsequent identification of the species as *C. salina* Wahlenb. (Saltmarsh Sedge) by authors JC, MD, ACJ and Arthur Chater is an exciting find and was reported by Dean *et al*. (2005). *C. salina* is a coastal species with an amphi-Atlantic distribution. It has a hybrid origin, the product of a cross between *C. paleacea* Schreb. ex Wahlenb. and *C. subspathacea* Wormsk., neither of which is recorded from the British Isles. Thus its discovery raises interesting questions on the distribution, dispersal and evolutionary potential of the species. This paper details what is currently known of the ecology, identification and distribution of the British population of the sedge, expanding upon the areas outlined by Dean *et al*. (2005). Additionally, it includes a detailed description of the sedge in Britain and the characteristics that separate *C. salina* from its close relatives. It also discusses the possible origins of the population and speculates on the reasons for its establishment.

DESCRIPTION AND IDENTIFICATION

When seen in its habitat as an extensive colony, *C. salina* can be confused from a distance with *Elytrigia juncea* (L.) Nevski. The following description is expanded from Jermy *et al.* (2007 Jermy *et al.*) following further field studies in Norway (PA) and Scotland (MD) and on N. American material (JC).

Rhizomes far-creeping; shoots tufted; roots rich brown-grey; scales red-brown, often blackened, persistent.

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Stems 16–30 cm, stiff, obtusely trigonous, smooth, spongy, typically shorter than the leaves of the vegetative shoots.

Leaves <30 cm (–60–70 cm where more sheltered) × 3–4 mm, mid-green, ± glaucous and matt on both surfaces, stiff, V-shaped, upper ⅓–½ and tip toothed; amphistomous; sheaths herbaceous, pale brown, soon decaying; inner face hyaline, transverse septa distinct; ligule acute, c. 5 mm; apex concave.

Inflorescence ¼ to almost ½ length of stem; lowest bract leafy, somewhat invaginated at the base, slightly shorter to slightly longer than inflorescence, often spathe-like, enclosing spike. Male spikes 1–2(–3), 1–2 cm long; male glumes 4–6 mm, oblanceolate-elliptic, blackish-brown; margins hyaline; apex obtuse.

Female spikes 2–3, 1–3 cm, erect; narrow, cylindrical, upper almost sessile, lowest spike with peduncle up to 1·5 cm, sometimes lax-flowered at base; female glumes 4–5 mm, ovate-elliptic, mostly as wide as the utricles or wider, green at the start of flowering and maturing to mid - to dark-brown with broad pale centre with obvious midrib, some glumes three-veined; margins sometimes asymmetrical in upper florets or tending to be retuse; apex of those in upper florets apiculate, lower florets all awned; awn ± 1 mm long, toothed. Utricles 2·5–3·5 mm × 1–2 mm, ellipsoid, apex acute, slightly papillose with 0–3 nerves beneath beak; beak 0·2–0·4 mm, mostly cylindrical, sometimes conical, lacking spinules around the beak orifice, obliquely truncate or not; stigmas 2; nut orbicular or obovate, apex truncate, biconvex, glossy, usually deeply constricted on one face. Fruiting occurs in June and July.

C. salina in Scotland is very sparse flowering. No fertile specimens were found in 2004–2006. Therefore the important characteristics of the truncate apex and constricted nut have not been seen in British material. Low fertility may partly be an intrinsic feature of the species. Other maritime members of section *Phacocystis* which have a hybrid origin exhibit lowered pollen fertility, partly as a result of disturbed meiosis (Cayouette and Morisset 1985). The few Norwegian populations examined failed to produce fertile seed. However, ecological factors may also influence fertility. Tidal inundation may cause a failure in pollination. Canadian *C. salina* populations which are covered by tides during summer exhibit sterility. By comparison, Canadian populations covered only, or mostly, by spring and autumn high tides can produce good seeds.

Within the British flora *C. salina* is closest in appearance to *C. recta* Boott which, however, has a different ecological niche to *C. salina*. *C. recta* is found along the edges of the higher reaches of estuaries, usually amongst tall vegetation, e.g. in the Oykel estuary it can be dominant with *Phragmites*, *Phalaris arundinacea* and other grasses in species-rich sedge communities of tall-herb fen (S27), with *C. rostrata*, *C. nigra* and *Juncus acutiflorus* (Jermy *et al*. 2007). In other places (e.g. Bonar Bridge) it may form extensive and dense populations, excluding any other species. By contrast, *C. salina* is found on the mid-to-llower saltmarsh where it frequently forms single-species stands up to 10 m by 3 m in the saltmarsh creeks. It also creeps into the *Puccinellia maritima* sward where it has shorter leaves, flowers very infrequently if at all, and is much sparser and could easily go undetected (Dean *et al*. 2005).

In Britain *C. salina* and *C. recta* are also geographically separate, *C. recta* being located on the northeast coast of Scotland, *C. salina* on the west. *C. recta* is a much larger plant typically up to 1 m tall with vegetative leaves up to 130 cm, whereas *C. salina* grows up to 30 cm unless the plant is in the shelter of creek banks where the leaves can be longer. Morphologically the two species are separated by the female spike length (1–3 cm in *C. salina* vs 2–8 cm in *C. recta*), longer and typically narrower female glumes with a more acuminate apex in *C. recta* (4–5 mm long in *C. salina* vs 3–7 mm in *C. recta*); the beak of *C. recta* tends to be shorter and narrower (0·2–0·4 mm in *C. salina* vs c. 0·2 mm in *C. recta*). Both have apiculate or awned female glumes, with the glumes from the lowest florets usually awned in both species.

Two other species within the same section, *C. subspathacea* and *C. vacillans* Drejer are broadly similar to *C. salina*, but a third species, *C. paleacea*, is relatively easy to distinguish. None of these three species have been recorded from Britain (Dean *et al*. 2005). *C. salina* is a larger plant than *C. subspathacea*, which is typically a very short stemmed (3–15 cm, although in some Hudson Bay and north-eastern North American populations it can grow as tall as 25–30cm), narrow leaved (1–3 mm), low growing early flowering species of saltmarshes. *C. paleacea* is a larger species than *C. salina* but smaller in stature than *C. recta*. *C. paleacea* is distinguished by its pendent female spikes and pale brown female glumes with a long, finely serrated awn 6–15 mm long (Mossberg & Stenberg 2003).

In size *C. vacillans* is closest to, but typically taller than, *C. salina*. The two species are also separated by utricle appearance. Specifically, *C. vacillans* has densely papillose and nerved utricles, with spinules around the beak orifice, dark pistillate glumes with a narrow central band, sometimes incomplete (not reaching the apex) on unawned glumes, usually a scabrous stem, and dull surfaced nuts. It also has some divergent to even drooping spikes and usually a sharp trigonous stem. *C. salina* lacks this suite of characters. Both share the characters of frequently scabrous awned glumes and constricted nuts.

Small plant size, spathe-like lowest bract and the female glumes, which are mostly found with a short to long scabrous awn, are the best character to identify *C. salina* and are consistent across specimens of *C. salina* in northern Europe (including Scotland) and eastern North America. A key to *C. salina* and closely related, potent-ially confusing species is given below.

KEY

A key to *Carex salina* and related coastal species in *Carex* section *Phacocystis* in northwest Europe.

This section is identified by separate male and female spikes with the upper usually entirely male and the lower usually entirely female, two stigmas, and utricles and nuts biconvex or planoconvex.

1. Vegetative leaves involute and 1–3 mm wide; leaves lying on substrate surface; on lower reaches of saltmarsh. ....……*Carex subspathacea*
1. Vegetative leaves keeled or V-shaped or widest more than 3 mm; leaves clear of substrate surface; on lower or upper reaches of saltmarsh or adjacent landward vegetation…............ 2

2. Stomata predominantly or exclusively on one leaf surface only ....……3
2. Stomata abundant on both leaf surfaces 6

3. Leaves with stomata predominantly or exclusively on upper surface; female glumes obtuse or acute, without awns 4
3. Leaves with stomata predominantly or exclusively on lower leaf surface; female glumes with prominent awn at least on lower florets.. 5

4. Lowest bract from shorter to slightly longer than inflorescence; stem usually scabrous below lowest spike; nuts dull ....……*Carex nigra*
4. Lowest bract (usually greatly) exceeding inflorescence; stem usually mostly smooth below lowest spike; nuts glossy or mostly so.. *Carex aquatilis*

5. Almost all female spikes pendent; all female glumes with prominent awn; awn up to 15 mm ....*Carex paleacea*
5. Female spikes erect or semi-erect; usually only lower florets awned; awn <5 mm...................... ....*Carex recta* (part)

6. Proximal bract often spathe-like, enclosing spike; nuts glossy ....*Carex salina*
6. Proximal bract not spathe-like; nuts glossy or dull 7

7. Female glumes with papillose midrib, midrib of unawned glumes not always reaching apex; nut dull .... …..*Carex vacillans*
7. Female glumes with midrib not or slightly papillose, midrib of unawned glumes reaching apex; nut usually glossy .... *Carex recta* (part)

DISTRIBUTION

C. salina is currently known from a single site in the British Isles, at Morvich at the head of Loch Duich (v.c. 105, Map ref. NG 9520, NG 9521). In 2006 17 other locations on the west coast of Scotland across two vice-counties (v.c. 98 and 105) were examined (Table 1 in appendix) but *C. salina* was not found at these sites.

The species is also recorded from the western and northern coasts of Norway and northwestern Russia, from Hudson Bay and St Lawrence River and the eastern coastal area of Canada (Chater in Tutin *et al*. 1980; Hultén & Fries 1986; Standley *et al*. 2002; Mossberg & Stenberg 2003).

There are also records from Greenland (Hultén & Fries 1986) and Iceland (Chater in Tutin *et al*. 1980; Hultén & Fries 1986). However, reports of *C. salina* from Greenland are based upon misidentifications. Cayouette & Catling (1992), reviewing Greenland *C. salina* specimens, considered them primarily to be C. *lyngbyei* × *nigra* hybrids with some *C. subspathacea* individuals. Reports of *C. salina* from Iceland are probably based upon Ostenfeld & Gröntved (1934) and Gröntved (1942) and reflect an earlier taxonomic treatment. More recently Löve (1983) did not report C. *salina* from Iceland and Hylander (1982) considered that *C. salina* from Iceland could perhaps refer to *C. lyngbyei* × *subspathacea* hybrids.

ECOLOGY

In its single Scottish locality, *C. salina* is present in creek channels, although it is absent in the main river channel, and along the low banks of the creeks, growing in the mid-lower region of the saltmarsh zonation (Dean *et al*. 2005). Associated plant species on the saltmarsh include: *Armeria maritima*, *Glaux maritima, Plantago maritima, Aster tripolium, Triglochin maritimum*, *Juncus gerardii, Blysmus rufus*, *Eleocharis palustris*, *E. uniglumis, Festuca rubra, Puccinellia maritima* and *Agrostis stolonifera*. In N.V.C. terms, this site consists of mainly SM13 *Puccinellia maritima* saltmarsh and SM16 *Festuca rubra* saltmarsh but also some patches of SM19 *Blysmus rufus* saltmarsh and S19 *Eleocharis palustris* swamp. *C. salina* plants are scattered over a wide area of the lower saltmarsh. It occurs as single-species stands on the silt and, more frequently, less densely as shoots among the *Puccinellia* sward. The sparsely flowering clones are growing near enough to mean high tide level to be regularly inundated.

The above is a very similar habitat to those where *C. salina* is found along the St Lawrence River, in eastern Québec, with many companion species in common. These include *Glaux maritima*, *Plantago maritima*, the *Triglochin maritimum* group, *Juncus gerardii*, *Blysmus rufus*, *Eleocharis palustris*, *Festuca rubra*, *Puccinellia* subsp. and *Agrostis stolonifera*. Not found alongside *C. salina* in Britain but frequent associates in the Canadian communities are: *Ranunculus cymbalaria*, *Salicornia* spp., *Argentina egedii* agg., *Carex paleacea* and *Hordeum jubatum*. By comparison, at the margins of pools in saltmarshes in James Bay and Hudson Bay, *Carex salina* grows with *Argentina egedii* agg., *Calamagrostis deschampsioides*, *Carex mackenziei*, ×*Dupoa labradorica*, *Festuca rubra*, *Montia fontana*, *Parnassia palustris*, *Rhinanthus minor* agg., *Stellaria crassifolia*, and *Triglochin maritimum* (Cayouette & Darbyshire 1993).

In Norway the species occurs as uniform stands on saltmarshes fed by river water and as tussocks at the back of coarse sandy beaches. It also occurs among *Puccinellia* dominated saltmarsh communities where *Puccinellia phryganodes, P. retroflexa*, *Triglochin maritimum, Plantago maritima, Aster tripolium, Agrostis stolonifera*, *Argentina egedii* agg. and *Stellaria humifusa* are associates (Nordhagen 1954; Fremstad 1997).

ORIGIN AND ESTABLISHMENT

The flora of any area is a dynamic entity with both losses and gains occurring over time due to stochastic effects (random or chance events) and changes mediated through biotic (the living components of the environment) and abiotic (the non-living components) factors. Nevertheless, it is tempting to speculate on both the origin of *C. salina* in Scotland and the reasons for its colonisation.

C. salina has evolved following hybridisation between two other members of *Carex* section *Phacocystis*, *C. paleacea* and *C. subspathacea* (Cayouette & Morisset 1985, 1986a, 1986b; Standley 1990). This mode of speciation is common in this group of sedges.

For instance, *C. recta* is a product of a cross between *C. paleacea* and *C. aquatilis* Wahlenb. (Cayouette & Morisset 1985, 1986a, 1986b; Standley 1990) while *C. vacillans* is the result of a cross between *C. paleacea* and *C. nigra* (L.) Reichard (Chater in Tutin *et al.* 1980; Cayouette & Catling 1992). Almost all the species above (*C. salina*, *C. recta*, *C. vacillans*, *C. paleacea* and *C. subspathacea*) inhabit saline and brackish seashore and estuarine habitats with the other two species, *C. aquatilis* and *C. nigra*, sometimes found on upper saltmarshes. The close proximity of the various species allows hybridisation to occur. This then provides an evolutionary mechanism through which the niches available in these open, dynamic, recently disturbed and glaciated areas can be exploited. These are of course classic conditions for hybrid speciation and establishment (Grant 1981).

With this mode of speciation it is possible that *C. salina* has evolved in situ. However, this seems distinctly improbable as neither of the parental species has been recorded from the British Isles. The absence of *C. subspathacea* from the British flora might be artificial, remaining undetected due to a combination of geographic isolation, unprepossessing habitat and predominantly very low-growing vegetative habit. By comparison, *C. paleacea* is highly unlikely to have escaped discovery, being a large, distinctive sedge occurring in single species stands on the strandline, although the presence of *C. recta* in Scotland, may mean that *C. paleacea* was part of the British flora in the past.

In general maritime habitats provide open niches that may be colonised by the limited number of species adapted to such harsh environments. Some species are able to rapidly exploit these niches and become widespread, for example *Spartina anglica* which has spread by natural colonisation and planting from its origin in about 1890 to cover a large part of the English and Welsh coastline (Leach 2002). *C. salina* may have been present on the west coast of Scotland for a long time especially as the species is very hard to detect, particularly when not growing in pure stands, a result of the inflorescence being markedly shorter than the vegetative shoots. However, the saltmarshes of western Scotland were extensively surveyed by Adam between 1972 and 1975 when neither *C. salina* nor either of its parental species were recorded (Adam 1978, 1981). The implication therefore is that *C. salina* has become established at Morvich following long-distance dispersal from Scandinavia or North America, possibly during the last thirty years. The Scottish location is probably the first area in the world where *C. salina* is apparently growing outside the ranges of both parental species.

Little is known of the dispersal ability of saltmarsh species, although the wide distribution of many saltmarsh species suggests that they are relatively easily dispersed (Adam 1990). It is possible that *C. salina* has spread through seed or rhizome via the sea. Praeger (1913) noted a high proportion of sedges with buoyant seeds, while Leck & Schutz (2005) list adaptations such as inflated utricles, corky pericarp and pericarps with air cells which enable the utricle to remain buoyant. Some dispersal of patches of vegetation by ice movement are common along the St Lawrence River, and parts of populations of *C. salina* and other rhizomatous species are moved locally (Cayouette & Morisset 1985). It is also possible that seeds or vegetative material could be transported by birds. Mueller & van der Valk (2002), in a study of wetland seed dispersal, found viable seed of *Carex* species in duck faeces. Migration routes of mallard (*Anas platyrhynchos*), for example, include Scandinavia to Scotland (Wernham *et al.* 2002). Due to the short retention time of seeds within the gut of waterbirds most seeds are expected to be ejected on route (Clausen *et al.* 2002) but Figuerola & Green (2002) consider that long-distance dispersal by endozoochory (internal dispersal of seeds) can occur. Epizoochory (dispersal of seeds externally attached to feathers, bills or feet) is also possible although there are no studies with precise data on distances and movements of birds (Figuerola & Green 2002). It is also possible that some plant material could be transported by boats, possibly in ballast, at least for part of the journey, with currents and tides doing the rest.

Assuming propagules of *C. salina* have been continually dispersed since the species' origin it is interesting to consider why the plant has possibly become established only recently. Saltmarshes are dynamic habitats and it is possible that postglacial isostatic rise may have facilitated sufficient change to allow *C. salina* to become established, although this may be offset by eustatic (worldwide) sea level increases in the near future. Perhaps more likely candidates as agents of saltmarsh change are the climatic factors beginning to influence the British Isles. Western Scotland is experiencing increasing extremes of rainfall with longer and heavier spells of precipitation occurring more frequently (Fowler & Kilsby 2003) along with generally stormier winters and calmer summers (Lozano *et al*. 2004). It is possible that these conditions cause disruption to the habitat akin to the effect of annual ice movement in Canada, which has allowed *C. salina* to become established.

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APPENDIX 1. SALTMARSHES SURVEYED ALONG THE WEST COAST OF SCOTLAND IN 2006

Saltmarshes	10 km square	1 km square(s)	v.c.
Carex salina present			
Morvich, eastern head of Loch Duich	NG92	NG9520, NG9521	105
Carex salina not found			
Nostie, Loch Duich	NG82	NG8526	105
Ardelve, Loch Duich	NG82	NG8726	105
Slumbay, Loch Carron	NG83	NG8939	105
Loch Kishorn	NG84	NG8341	105
Head of Loch Torridon	NG85	NG8854, NG8954, NG8955	105
Shiel Bridge, southern head of Loch Duich	NG91	NG9318, NG9319	105
Head of Loch Long	NG93	NG9230	105
Head of Loch Carron	NG94	NG9241	105
Head of Loch Craignish	NM80	NM8205	98
Head of Loch Melfort	NM81	NM8412	98
Kilninver	NM82	NM8222	98
Dunstaffnage	NM83	NM8733, NM8833	98
An Seilan	NM83	NM8939	98
Balure of Shian	NM94	NM9041	98
Portnacroish	NM94	NM9246	98
Dalrannoch	NM94	NM9340, NM9341	98
Head of Loch Creran	NN04	NN0044, NN0045	98