

## Could *Centaurium scilloides* (L. f.) Samp. (Gentianaceae), Perennial Centaury, have colonised Britain by sea?

T. C. G. RICH

*Department of Biodiversity and Systematic Biology, National Museums & Galleries of Wales,  
Cardiff CF10 3NP*

### ABSTRACT

The hypothesis that the disjunct distribution pattern of the western European endemic *Centaurium scilloides* can be explained by dispersal of seeds in sea water has been tested. The Welsh genotype was found to be self-compatible and one plant produced 11500 seeds in its second year alone. About one third of the seeds floated in sea water for up to 14 days, and 18% of seeds floated for at least 28 days, and they retained 95% viability. The results are consistent with, but do not prove, the hypothesis that *C. scilloides* could have colonised Britain by sea.

KEYWORDS: Dispersal, germination, pollination.

### INTRODUCTION

The western European endemic *Centaurium scilloides* (L. f.) Samp. (Gentianaceae), Perennial Centaury has a series of disjunct populations scattered up the Atlantic coasts from Portugal to Wales, and occurs in the Azores (Figure 1; Rich *et al.* 2005). This disjunct distribution pattern could be relict from fragmentation of a more continuous distribution earlier in this interglacial, or could have resulted from a series of dispersal events from southern donor colonies to new sites in the north after the last glaciation. The latter has been found for coastal species such as *Cakile maritima*, *Carex arenaria* and *Eryngium maritimum* which are believed to have survived the last glaciation in refuges in SW Europe and North Africa, and have since re-colonised northern Europe showing decreasing genetic diversity northwards (Clausing *et al.* 2000, Jonsson & Prentice 2000).

In Britain *Centaurium scilloides* is currently only known from one native site in Pembrokeshire, Wales, where it is locally frequent along about 3 km of dune and sea cliff; it also formerly occurred at two sites in Cornwall, one near Land's End and the second on the north Cornish coast (Rich *et al.* 2005). These British localities are somewhat isolated from the French and Spanish populations (the nearest populations occurring in Normandy and Brittany), but their coastal location suggests that dispersal to them could have occurred by seeds floating in the sea from France. The seeds of *C. scilloides* are *c.* 0.3–0.4 mm diameter and have no obvious dispersal mechanism other than being shaken out of the fruiting capsules. Tchernia (1980) provided maps of February surface currents in the Atlantic Ocean, which are also summarised in Figure 1 (his maps are amongst the most detailed available, and likely to be representative of summer currents when seeds would be dispersed). There is a general clockwise water circulation driven by the North Atlantic Drift current, with a divergence south-west of Ireland, and local circulation within the Bay of Biscay. Overall, the frequency of the currents is somewhat irregular (Tchernia 1980). Local currents may differ from the overall picture, and Nelson (2000) gives a more detailed map of sea currents for Britain: in south-west Britain there are easterly currents from Dorset eastwards, westerly water movements along the south Devon and Cornish coasts, and northerly currents along the north Cornish and Devon coasts towards Wales and the Irish Sea. The combined directions of the Atlantic and local sea currents indicates that there is potential for sea water currents to account for at least some of the observed distribution pattern of *C. scilloides*, though it should be noted that the currents at the time that dispersal might have originally happened may be different to what they are now.

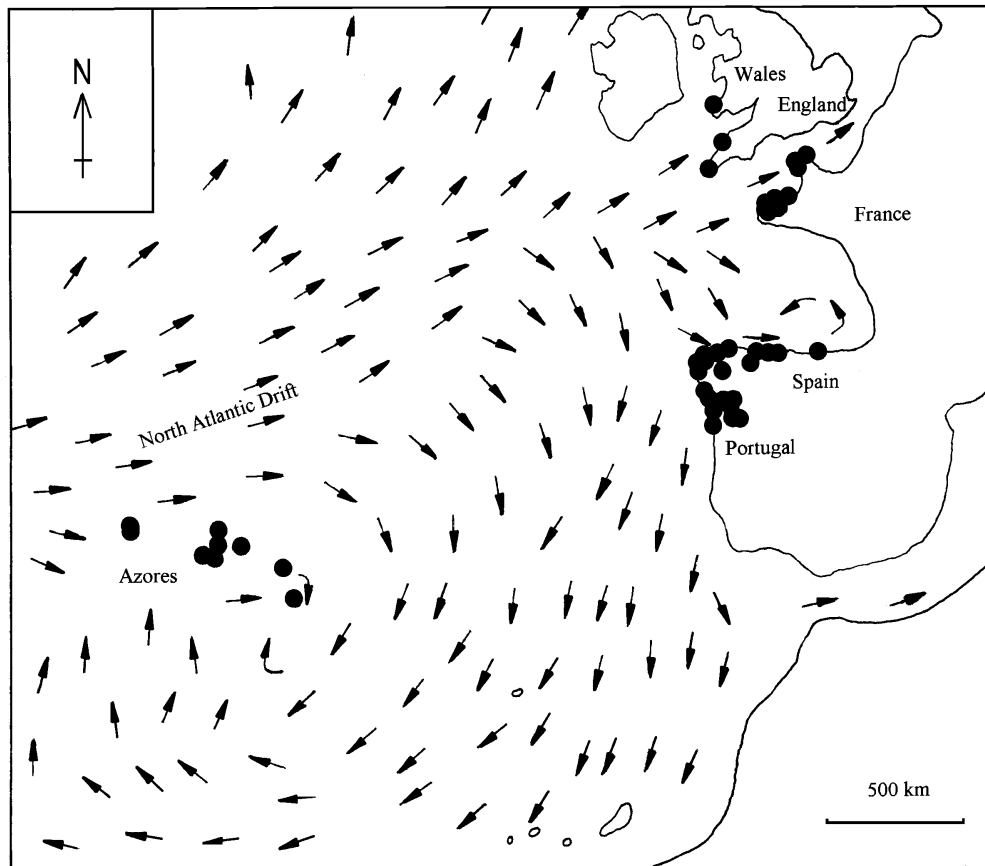


FIGURE 1. Distribution of *Centaurium scilloides* (•, after Rich *et al.* 2005) and direction of February surface water currents in the Atlantic Ocean (→, redrawn from Tchernia 1980).

For the distribution pattern to be explained by dispersal in the sea, two predictions would have to be met. First, seeds must float in sea water and remain viable. Second, to establish a population from a single seed, individual plants should also be self-compatible and produce fertile seeds. Observations and experiments were carried out to test these two predictions.

#### METHODS

One plant was grown from seed collected from the sea cliffs north of Newport, Pembrokeshire, Wales and cultivated by itself in an open, unheated greenhouse in Cardiff (the Cornish genotypes could not be tested as the populations are extinct). The plant flowered profusely in its second year, when observations were made on its floral biology by following marked flowers through their development. Four flowers had anthers removed in bud before anthesis. At the end of the summer, capsules were harvested and the mature seeds counted. The number of seeds per capsule was compared with seed production from the wild populations at Newport with open pollination, and with another plant from Sussex with open pollination, cultivated at the National Botanic Garden of Wales.

The harvested seeds were stored for about eight weeks at room temperature before being used for the flotation experiments. Samples of 100 seeds were dropped into *c.* 75 ml of sea or fresh

water in white plastic beakers and stirred to simulate wave action. Pots were stirred again each day, and the number of seeds floating counted after stirring. Water volumes were maintained by topping up the beakers with tap water.

For the germination experiments, all seeds (floating and submerged) were taken from the beakers and flushed with fresh tap water, and then placed on wet filter papers in Petri dishes in warm and light conditions to germinate. After a month, minor mould development began on the filter paper in some dishes. The germination experiment was terminated after three months.

## RESULTS

The single isolated plant of *C. scilloides* flowered profusely in its second year, producing 59 flowers between June and August. It set abundant seed (Table 1) and it is therefore self-compatible. Extrapolation from counted samples indicates that this one plant produced about 11500 seeds in this second year. It is a polycarpic perennial and flowered even more profusely in its third year. Removal of the anthers from unopened flowers resulted in a reduction in mean seed set of about 40% (Table 1), indicating that some cross-pollination must have occurred for them to set seed, though no pollinators were observed visiting the flowers. A comparison of the numbers of seeds per capsule from this cultivated plant with capsules collected from wild populations with open pollination shows that the seed set per capsule is very similar (Table 1), though again rates of self- and cross-pollination are not known.

Observations on the floral biology showed that individual flowers followed the same general sequence but varied in rate of development. In bud, the stigma is located at about the middle of, and between, the undehisced anthers. The flowers open in bright weather by mid-morning and close in the evening; they may remain closed all day in very dull or in wet weather. The flowers are about 17–18 mm in diameter, are slightly cupped and have a bright pink corolla but have no discernible scent. The bright yellow anthers dehisce in sequence, slowly twisting and curling exposing yellow pollen on the outer sides, and the filaments slowly elongate. The stigma and style initially may or may not be bent slightly to one side of the stamens, and may or may not move upright during the day and come into contact with the anthers, but the stigma does not appear to be receptive at this stage. Three, four or all five anthers may dehisce in turn on the first day, any remaining anthers dehiscing the following day. By the third day, the filaments have elongated taking the dehisced anthers above the level of the stigma, which again may or may not be strongly bent to one side. The stigma becomes strongly bi-lobed on the third day when, presumably, it becomes receptive to pollen. The flowers may open for a further two days with the stigma in similar condition. When the flowers close, they may force the stigma to come into contact with the anthers thus allowing self-pollination, and pollen may also be deposited on the petals. Four to seven days after opening, the flowers close and do not open again, and the pink coloration fades whitish. The flowers thus are adapted for cross-pollination if there are suitable pollinators, but will self-pollinate if not cross-pollinated.

TABLE 1. NUMBER OF SEEDS PER CAPSULE OF *CENTAURIUM SCILLOIDES* WITH VARIOUS POLLINATION TREATMENTS

Source	Treatment	Number of seeds per capsule	Mean
Newport, cultivated plant	Isolated plant, intact flowers, open pollination	83, 169, 177, 196, 203, 224, 245, 261	195
Newport, cultivated plant	Isolated plant, anthers removed, open pollination	4, 103, 171, 199	119
Newport, wild population 1	Open pollination	163, 214, 243, 281	225
Newport, wild population 2	Open pollination	142, 174, 194, 239	187
Newport, wild population 3	Open pollination	9*, 185, 264, 271	199
Sussex, cultivated plant	Open pollination	93, 120, 157, 184	139

\* small atypical capsule

TABLE 2. NUMBER OF SEEDS FLOATING IN SEA AND FRESH WATER WITH TIME, WITH FINAL PERCENTAGE GERMINATION

Treatment	1 day	2 days	4 days	7 days	14 days	21 days	28 days	final germination
Control	-	-	-	-	-	-	-	80%
Sea water + detergent	0	-	-	-	-	-	-	-
Fresh water + detergent	0	-	-	-	-	-	-	-
14 days fresh water	70	68	64	60	30	-	-	86%
21 days fresh water*	32	31	31	28	19	3	-	95%
1 day sea water	41	-	-	-	-	-	-	78%
2 days sea water	41	39	-	-	-	-	-	72%
4 days sea water	55	55	49	-	-	-	-	88%
7 days sea water	42	41	39	38	-	-	-	88%
14 days sea water	68	59	59	56	47	-	-	93%
28 days sea water	54	54	53	48	30	19	18	95%
Average	50.4	49.6	49.2	46	31.5	11	18	87%

\* Initially planned for 28 days but terminated following significant germination under water.

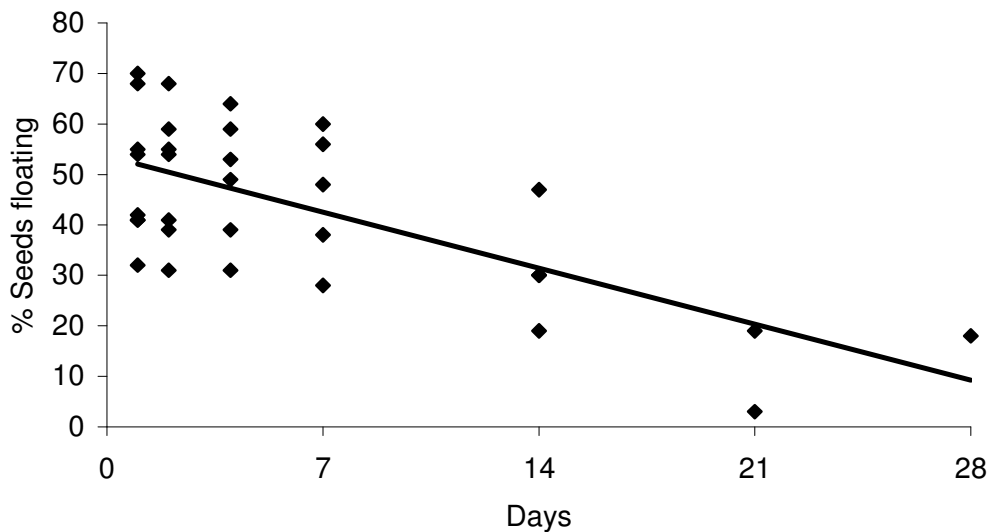


FIGURE 2. Number of seeds floating with time for all treatments. A best fit line is also shown

The numbers of seed floating with time for each treatment is shown in Table 2 and plotted in Figure 2. About 66% of the seeds floated initially, but a further third sank on first stirring. Groups of 5–15 seeds often floated together. Addition of a small drop of household detergent to additional samples of 100 seeds in both sea and fresh water resulted in all seeds sinking immediately, indicating the role of surface tension in flotation. About one third of the seeds floated in sea water for up to 14 days, but stirring is a poor substitute for turbulent water at sea. 18% of seeds floated for at least 28 days in sea water, and retained high viability in all treatments (mean 87%; Table 2).

Germination was first observed after 18 days in the Petri dishes. After 20 days a large flush of

germination was also observed happening under water in the 28 days fresh water treatment, which was therefore terminated and the seeds were transferred to a Petri dish for further germination. Seeds from sea water and control treatments germinated slowly over time, typically 3–4 per day, rather than in one flush. The final percentage germination was generally very high (Table 2), with both the three weeks fresh water and four weeks sea water treatments achieving 95% germination. There was an interesting minor trend suggesting that the longer the immersion in water the higher the percentage germination (for all treatments combined  $r = 0.82$ , 7 d.f.,  $p = 0.01$ ).

## DISCUSSION

The pollination and flotation results are consistent with, but do not prove, the hypothesis that *C. scilloides* could have colonised Britain by sea from French populations. The Welsh genotype of *Centaurium scilloides* is self-compatible, and the one plant produced thousands of viable seeds in its second (and subsequent) year; the Welsh populations could therefore establish from a single seed. Seeds can float in sea and fresh water by surface tension for significant periods of time, and they are still viable after immersion in sea water for at least four weeks. Extrapolation of the best fit line in Figure 2 suggests that they would float for only five weeks. Seeds of quite a number of plants are well known to float in sea water and remain viable, at least for short periods (Nelson 2000). Dispersal by sea is thus most likely to have been by a series of short sea current dispersal events, perhaps from Brittany or Normandy to Cornwall and then to Wales, rather than by multiple long distance events.

Whether dispersal by sea from the mainland could also explain the localities in the Azores is another matter. The Azores populations differs from the mainland European populations in being generally white-flowered and with narrow leaves, and are likely to be derived from the mainland population rather than *vice versa* (Rich *et al.* 2005). The Azores lie about 1300 km west of Portugal, and, given that the currents between the Azores and mainland Europe are typically less than 12 nautical miles per day (Tchernia 1980), seeds would perhaps have to float for four months to reach the Azores. Schäfer (2003) thought *C. scilloides* seeds were dispersed by both wind and water, but he regarded dispersal by birds as the main mechanism by which native species have arrived on the Azores, with wind dispersal uncommon and sea dispersal rare. It is also possible that *C. scilloides* could also have arrived in Britain by birds or wind.

## ACKNOWLEDGMENTS

I would like to thank Jim Wild for collecting the sea water, Kate Pryor for data on seed production in the wild, Helen Proctor for collecting cultivated material from Sussex, Gillian and Tom Jones for watering the greenhouse, and Andy Mackie for discussion of sea currents.

## REFERENCES

- BOUMAN, F., COBB, L., DEVENTE, N., GOETHALS, V., MASS, P. J. M. & SMETS, E. (2002). The seeds of Gentianaceae, in STRUWE, L. & ALBERT, V. A., eds., *Gentianaceae: systematics and natural history*, pp. 498–572. Cambridge University Press, Cambridge.
- CLAUSING, G., VICKERS, K. & KADEREIT, J. W. (2000). Historical biogeography in a linear system: genetic variation in Sea Rocket (*Cakile maritima*) and Sea Holly (*Eryngium maritimum*) along European coasts. *Molecular Ecology* **9**: 1823–1833.
- JONSSON, B. O. & PRENTICE, H. C. (2000). Allozyme diversity and geographic variation in the widespread coastal sedge, *Carex arenaria*. *Diversity and Distributions* **6**: 65–80.
- NELSON, E. C. (2000). *Sea beans and nickar nuts*. B.S.B.I. Handbook no. 10. B.S.B.I., London.
- RICH, T. C. G., EVANS, S. B., EVANS, A. E., MAGNANON, S., HOPKINS, F., CALDAS, F. B., PRYOR, K. V. & LLEDÓ, M. D. (2005). Distribution of the western European endemic *Centaurium scilloides* (L. f.) Samp. (Gentianaceae), Perennial Centaury. *Watsonia* **25**: 275–281.
- SCHÄFER, H. (2003). *Chorology and diversity of the Azorean flora*. Dissertationes Botanicae 374. J. Cramer, Stuttgart.
- TCHERNIA, P. (1980). *Descriptive regional oceanography*. Pergamon Marine Series Volume 3. Pergamon Press, Oxford.

(Accepted May 2005)

