Ipomoea tiliacea (Convolvulaceae) seeds stranded on the south-west coast of Ireland

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Abstract

Three 4 mm drift seeds collected from St Finan's Bay on the south-west coast of Ireland were cultivated to produce climbing plants with cordate to trilobed leaves. The sequence of the Internal Transcribed Spacer region of ribosomal DNA of these plants provided a match for *Ipomoea tiliacea* (Willd.) Choisy. This plant is native from the Bahamas to southern Brazil, commonly occurring in maritime regions of the mainland and islands. This is the first record of seeds of this species likely to have been carried across the surface of the North Atlantic Ocean. Records of this plant, elsewhere in Europe, require confirmation.

Keywords: Ocean drift; ribosomal DNA; germination; disseminule; long-distance dispersal

Introduction

Strandings of disseminules originating from the Americas were first recorded from Irish shores by Colgan (1916), although the origin of such drift to European shores was first recognised by Sloane (1698). Drift disseminules have been recorded from Svalbard and Novaya Zemlya, in the Arctic, southwards to the Macaronesian Islands (Cadée & Dijksen, 1999; Nelson, 2000). Most of these specimens will have been recorded on account of their large size, those within the Fabaceae being the most frequently stranded disseminules found in collections. Smaller seeds of Fabaceae have also been reported as strandings, ranging from regularly stranded 3 to 6 mm seeds of *Lathyrus japonicus* var. *maritimus* (L.) J.T.Kartesz & Gandhiand to the rare 5 mm seed of *Vigna luteola* (Jacq.) Benth. (Minchin *et al.*, 2023).

Generally under-recorded as strandings are seeds within the Convolvulaceae which are typically less than ~1 cm, and so likely to be overlooked. There is the exception of *Merremia discoidesperma* (Donn.Sm.) O'Donell that can attain ~2.5 cm in diameter and has been recognised over some centuries on account of its ethnocultural significance due to a cross indentation on the seed coat (Nelson, 2000), which is due to one seed occupying the space of four within a fruit capsule (Gunn & Dennis, 1999).

Within the Convolvulaceae, Nelson (2000) recorded seeds of *Calystegia sepium* (L.) R.Br. subspecies that may have been involved in Long Distance Dispersal (LDD)

from temperate North America. Other members of this family that are found in tropical and subtropical regions of the Americas, include species of *Operculina* Silva Manso (Dan Austin in Nelson, 2000) and *Ipomoea* L., including *Ipomoea alba* L. and *I. pes-caprae* (L.) R.Br., which are well-known for producing seeds that strand widely within the Northeast Atlantic Ocean (Nelson, 2000) and in circum-tropical regions (Gunn & Dennis, 1999).

Within the Convolvulaceae many seeds of <3 mm, that might be transmitted by ocean currents are sufficiently small to be overlooked if stranded or do not survive oceanic transmission. On account of the similarity of many of the seeds within *Ipomoea* clades, and the large numbers of their species within the New World (Wood *et al.*, 2020), identification of seeds alone is difficult especially when important identification features, such as the distribution of hairs on the seed coat (Gunn, 1969) are almost certainly lost during an oceanic transit. Such is the current knowledge of small drift disseminules and it is likely that further strandings of seeds within this family have yet to be identified.

To undertake a sea-journey a seed needs to be buoyant with a testa resistant to sea water. In Convolvulaceae this is due to gasses retained within the seed (Gunn & Dennis, 1999). Even though buoyant, biofouling accumulation could lead to sinking; losses may also occur from eventual seepage of sea water via the micropyle or from damage or losses from predatory activity. Furthermore, the environmental conditions on arrival may also not be conducive for germination, precluding establishment.

In this study we show that seeds of a member of the Convolvulaceae stranded on Irish shores could be germinated and subsequently identified to species using molecular techniques. By providing suitably controlled conditions, germination of stranded seeds was possible, enabling vegetative features to be described and leaf material used to sample genetic markers for identification.

The collection site

St Finan's Bay, Co Kerry, Ireland (51.84388, -10.33638) is a south-west Atlantic coastal bay, of almost 3.5 km in width, that in-part funnels drift towards a sandy bay of ~150 m in length. The bedrock of Upper Carboniferous shales has a north-east to south-west axis. Temperature maximum ranges of -1.5 to 28.1 °C at Valentia Observatory and 1508 mm annual rainfall. The bay is exposed to a transition between polar and tropical maritime air masses The surrounding area has poor acid soils with drainage into the beach area.

Methods

Seeds were collected over two days in November 2021 from the high shore. Five of the smaller seeds were selected, scarified with a knife, held in water overnight and sown indoors on 10 April 2022 within an incubator maintained at a temperature ranging 18 to 22°C. Each seed was placed in a separate pot using 50 % vermiculite and 50% compost. Three plants were re-potted and provided with a cane for climbing following the appearance of cotyledon leaves. Plants were re-potted and placed outside on 20 May 2022. Plants were removed and dried on 17 June 2022.

Strandings from the period 2021 and 2022 from St Finan's Bay were used to compare the overall sizes of seeds to include the five used in this study.

Leaves were measured using Vernier callipers from the base of the leaf sinus to the most apical extent, down to the nearest mm. Representative leaf forms were photographed on 20 May 2022. Plants were pressed 17 June 2022.

One of the three plants cultivated was submitted to the herbarium at the National Botanic Gardens, Dublin as: *Ipomoea tiliacea* (Willd.) Choisy, St Finan's Beach (H1), 17/06/2022: **DBN0044196.**

Genetic methods

Sample leaves from each of the three dried herbarium specimens were used for genetic analysis. DNA extraction, PCR and sequencing protocols followed those described for the Internal Transcribed Spacer region of nuclear ribosomal DNA (ITS) by Williams *et al.* (2014). The ITS region was amplified as a single fragment using the primers AB101 and AB102 (Douzery *et al.*, 1999).

CodonCode Aligner v. 11 (CodonCode Corporation, MA, USA) was used to edit and assemble sequences. An initial blast search was performed using Genbank (Benson *et al.*, 2013) to provide a preliminary taxonomic placement for the resulting sequences and *Ipomoea batatas* was identified as the closest match in each case.

ITS sequences for species in the *Ipomoea batatas* group as circumscribed by Wood *et al.* (2020) were then downloaded to generate an alignment against which the stranding sample sequences could be compared. The species included were as follows: *I. batatas* (L.) Lam. (20 samples), *I. cordatotriloba* Dennst. (10 samples), *I. cryptica* J.R.I.Wood & Scotland (6 samples), *I. cynanchifolia* Meisn. (6 samples), *I. grandifolia* (Dammer) O'Donell (7 samples), *I. lacunosa* L. (10 samples), *I. leucantha* Jacq. (6 samples), *I. littoralis* Blume (6 samples), *I. ramosissima* (Poir.) Choisy (16 samples), *I. splendor-sylvae* House (1 sample), *I. tenuissima* Choisy (3 samples), *I. tiliacea* (Willd.) Choisy (9 samples), *I. trifida* (Kunth) G.Don (20 samples), and *I. triloba* L. (12 samples).

The alignment included multiple accessions for all species except *I. splendor-sylvae* which was represented by one sample. In total, 132 sequences were included (see Table 1 for details of GenBank accession numbers). The only member of the *I. batatas* complex not represented was *I. australis* (O'Donell) J.R.I.Wood & P.Muñoz, a species occurring in Argentina, Paraguay, Bolivia and rarely in Brazil (Wood *et al.*, 2020). There were no sequences of this taxon available on Genbank.

Sequences from the St Finan's Bay samples were aligned against a 399bp fragment of the ITS region that spanned part of the ITS1 region, the 5.8s region and part of the ITS2 region. This region was selected as it was present in all 132 samples in the analysis. Se-al v.20a11 (Rambaut, 2002) was used to generate the alignment.

Results

Of the five seeds sown, three germinated between 24 April to 5 May 2022. The brown seeds ranged from the globose 4.4 mm in length and 4.7 mm diameter (seed C) to the wedge-shaped seeds of A and B at 4.1 mm in length and 3.9 to 3.7 mm diameter (Fig. 1). Seed C had a round *Ipomoea*-type hilum (Gunn, 1969) of 1.4 mm diameter across the hilar pad. This was 1.0 mm in the remaining seeds that germinated.



Figure 1. Seeds planted on 10 March 2022. Seeds A, B and C germinated

Plant B was the last to germinate to produced tri-lobed to strongly tri-lobed leaves following the third node. The other two plants produced cordate leaves and all had a broad shallow leaf sinus and acuminate to aristate apices. Leaf venation at the base radiated into the lateral lobes and thereafter alternately to either side of the central vein. Leaf sizes ranged up to 8.5 cm in length from the base of the sinus to the leaf apex. All plants were vigorous anticlockwise climbers. Leaves of A and B and the plant C were pressed on 17 June 2022 (Fig. 2).





Sequences from the three specimens were deposited in GenBank with the following accession numbers: PP758396, PP758397 and PP758398. The 399bp alignment used for comparison of the St Finan's Bay specimens with published sequences of the *I. batatas* complex is available at https://doi.org/10.5519/gtiufsxn (see also Supplementary Material). One hundred and forty-six variable sites were observed although the majority were unicates and there were 62 variable sites when unicates were excluded.

Sequences of all three plants grown from the St Finan's Bay seeds (A, B and C) were identical. The similarity of those sequences to species in the *I. batatas* complex ranged from 90-100% (Table 1). Ninety percent similarity was observed with the *I. cryptica* sequences included in the analysis and 96% with *I. littoralis* and *I. splendor-sylvae*. For *I. cynanchifolia, I. cordatrilobata, I. grandifolia, I. leucantha, I. ramossisima* and *I. tenuissima, I. trifida* and *I. tribola,* 98% similarity was observed. *Ipomoea batatas* and *I. lacunosa* both showed infraspecific variation with 97-99% and 98-99% similarity observed respectively. Finally, all nine *I. tiliacea* sequences

included in the analysis were identical and they showed 100% similarly with the St Finan's Bay samples.

Discussion

Sequences of the ITS region from plants grown from three seeds discovered on the shoreline at St Finan's Bay, Co Kerry were found to match I. tiliacea, a member of the *I. batatas* complex as evidenced by the 100% match to sequences of that species deposited on Genbank. The sequences with which the newly generated sequences were compared included sequences from the recent monograph of American *Ipomea* by Wood *et al.* (2020). The other species of the *I. batatas* complex showed between 90 and 99% similarity with the sequences obtained from stranded seeds and for members of the complex occurring in coastal areas, sequence similarity was 96% for *I. littoralis*, 98% for *I. triloba* and 97-99% for *I. batatas.* Morphologically, Wood *et al.* (2020) noted that *I. tiliacea* is nearly always completely glabrous and with unlobed leaves. The leaves of plant B, grown from the stranded seeds, were trilobed (Fig. 3). While this may appear incongruent with the placement of these specimens in *I. tiliacea*, there is considerable leaf plasticity in *Ipomoea* and especially the *I. batatas* clade and trilobed leaves are not entirely unexpected in *I. tiliacea* (J.R.I. Wood, pers. com.). The seed morphology of the three specimens is also not entirely consistent with the description provided by Wood et al. (2020) since they are dark-brown and lack hairs whereas in the description of Wood et al. (2020), the seeds of I. tiliacea are black with short pubescent hairs in the angles. Hairs of varying length are found on seeds of many Ipomoea species that include I. pes-caprae (Gunn, 1969), widely spread about the world (Miryeganeh et al. 2014). However, seeds of this and other species of Convolvulaceae stranded on Floridian and Irish shores have been devoid of hairs (DM pers. ob.). Most probably these will have been shed while in transit and so hairs are not a useful feature for the identification of stranded seeds.

The variability in the seeds observed in this study may reflect differences related to the number of seeds that develop within a fruit capsule. Normally within the Convolvulaceae four seeds are produced within a fruit. Should some ovules fail to develop this can result in a seed at maturity having different shapes according to the number present. Fruits with three or four seeds grow with flattened adjacent seed faces (Staples *et al.*, 2020) and this is like the result for the seeds A and B. The larger globular seed C may be due one or two seeds within a fruit capsule.

In its native range, *Ipomoea tiliacea* typically occurs within a few kilometres of the coast in the Caribbean, in central America south from Veracruz, and in South America, from the Caribbean and Atlantic coasts south to Rio Grande do Sul. Its distribution and ecology make such an arrival of this species in western Europe possible. While not a shore species, its proximity to the coast could result in seeds becoming dispersed downstream, perhaps aided by storm events. Provided some remain buoyant for some months, such a trans-Atlantic transmission might take place. While buoyancy duration has not been reported for this species, *I. tiliacea* is within the same clade as *I. batatas* which has seeds of a similar size (3 -5 mm diameter) that are resistant to seawater immersion of 120 days and can subsequently germinate (Pereira *et al.*, 2020). The current study provides some evidence that *I. tiliacea* may be added to the list of other members of the Convolvulaceae with this capability.

Seeds of Convolvulaceae can be spread widely to become stranded on exposed shores and often in greater numbers than other dissemules. Ridley (1930) stated that within the Convolvulaceae seeds of *Operculina turpethum* (L.) Silva Manso were capable of floating for months thereby enabling its spread between islands within the Pacific Ocean. Staples *et al.* (2020) stated this was possibly a form of dispersal for all species within *Operculina* as it has a widespread distribution on islands. Dan Austin (in Nelson, 2020) found seeds believed to be of an *Operculina* species on a Co Kerry shore (H1) that was distinguished by having the larger a seed of 6 to 7 mm in length and a hilum 1.5 mm diameter, as keyed out in Nelson (2000). It is notable also that Muñoz *et al.* (2018) suggested that the arrival of the sweet potato (*I. batatas*) in the islands of Polynesia pre-dates the arrival of humans on the islands, plausibly by LDD by sea currents.

While species from the tropical Americas such as *I. tiliacea* are capable of dispersal by sea, few are capable of establishing themselves in temperate environments once stranded due to unsuitable environmental conditions. However, as this study shows, their seeds may still be viable and possible to cultivate.

This is the first occurrence of this species arriving as a viable seed in Northern Europe, following what is likely to have been a trans-Atlantic journey. The three cultivated seeds, being of the same species, indicate that *I. tiliacea* is in all probability frequently stranded on Irish Atlantic shores.

Similar sized brown wedge-shaped seeds have been recovered from the Atlantic beaches in Cos. Donegal (H35), Clare (H9), Kerry (H1) and Cork (H3). These are also likely to have resulted from drift from the Americas, being among many disseminules of different families recorded making such a crossing to Ireland for over a century (Colgan, 1916; Nelson, 1978, 2000) as well as elsewhere in Europe and mid-Atlantic islands (Minchin & Quigley, 2023).

According to Wood *et al.* (2000) there have been European records of *I. tiliacea*, however, these may have been confused for *I. littoralis*. The sequences generated in this study did not match that species. The records of three seeds from the south-west coast of Ireland that produced leaves represent the first confirmed accounts of *I. tiliacea* in Europe, albeit, as drifted seed from the New World. The record of three viable seeds in this study suggests that seeds of *I. tiliacea*, are not only capable of a North Atlantic transit and but that they are unlikely to be rare stranding events.

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Figure 3. Ipomoea tiliacea herbarium (plant B) lodged with DBN

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Table 1. Sequences of the fifteen species of the *I. batatas* group used to compare ITS sequences of plants grown from seeds stranded at St Finan's Bay. GenBank accession numbers are given for each sequence included with the total number of sequences per taxon also indicated. Percentage sequence similarity with the St Finan's Bay sequences for the 399bp ITS fragment analysed is also shown for each species.

Taxon	Number of samples	Sequence similarity to St Finan's Bay samples	GenBank accession numbers
<i>I. batatas</i> (L.) Lam.	20	97-99%	GQ249409.1; HM014433.1; JQ316197.1; KC621802.1; KC621806.1; KC621807.1; KC621808.1; KC621809.1; KC621810.1; KC621811.1; KC621812.1; KC621813.1; KC621814.1; KC621815.1; KC621816.1; KC621863.1; KC621864.1; MH189727.1; MH189728.1; MH189729.1
<i>I.</i> <i>cordatotriloba</i> Dennst.	10	98%	AF110939.1; JX423795.1; MN825096.1; MN825097.1; MN825098.1; MN825099.1; MN825100.1; MN825101.1; MN825102.1; MN825103.1
<i>I. cryptica</i> J.R.I.Wood & Scotland	6	90%	MN825139.1; MN825140.1; MN825141.1; MN825142.1; MN825143.1; MN825144.1
<i>I. cynanchifolia</i> Meisn.	6	98%	MN825154.1; MN825155.1; MN825156.1; MN825157.1; MN825158.1; MN825160.1
<i>I. grandifolia</i> (Dammer) O'Donell	7	98%	MN825253.1; MN825254.1; MN825255.1; MN825256.1; MN825257.1; MN825258.1; MN825260.1
<i>I. lacunosa</i> L.	10	99%	AF110937.1; DQ005997.1; DQ355324.1; JX423796.1; KY968870.1; KY968889.1; MH189735.1; MH189736.1; MH189737.1; MH189738.1
<i>I. leucantha</i> Jacq. (= <i>I.</i> × <i>leucantha</i>)	6	98%	KC621858.1; KC621860.1; MN825409.1; MN825410.1; MN825413.1; MN825414.1
<i>I. littoralis</i> Blume	6	96%	KP261924.1; MG752967.1; MN825434.1; MN825436.1; MN825437.1; MN825438.1
<i>I.</i> <i>ramosissima</i> (Poir.) Choisy	16	98%	DQ355323.1; MN825761.1; MN825762.1; MN825763.1; MN825764.1; MN825765.1; MN825766.1; MN825767.1;

		MN825768.1; MN825769.1;
		MN825772.1; MN825774.1;
		MN825775.1; MN825776.1;
		MN825777.1; MN825778.1
1	96%	MN825894.1
	000/	
3	98%	DQ355322.1; MG752962.2; MN825957.1
9	100%	DQ355321.1; KC621800.1; KC621801.1;
		MN825967.1; MN825968.1;
		MN825969.1; MN825970.1;
		MN825971.1; MN825973.1
20	98%	KC621833.1; KC621834.1; KC621835.1;
		KC621836.1; KC621837.1; KC621838.1;
		KC621839.1; KC621840.1; KC621841.1;
		KC621842.1; KC621843.1; KC621844.1;
		KC621845.1; KC621846.1; KC621847.1;
		KC621848.1; KC621849.1; KC621850.1;
		KC621851.1; KC621852.1
12	98%	KC621855.1; KC621856.1; KC621857.1;
		KC621859.1; KC621861.1; KC621862.1;
		KY968867.1; KY968868.1; KY968875.1;
		KY968878.1; KY968885.1; KY968904.1
	3 9 20	3 98% 9 100% 20 98%