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Evaluating records of trans-Atlantic dispersal to European shores of drifting disseminules

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Abstract

Disseminules drift across the North Atlantic Ocean from the Americas to the coasts of Europe with strandings recorded on the shores of the Arctic Ocean southwards to the Macaronesian and Azores islands. The parent plants inhabit vegetation ranging from tropical wetland forests to temperate strandlines and coastal dunes. Their disseminules undergo different ocean crossing times according to size and buoyancy. We use drifting plastics as a surrogate for the likely risks that disseminules face during long-distance oceanic spread. While the disseminules originate in habitats spanning a wide latitudinal range, we have compared the records of the massed strandings on beaches in Florida, less frequently in Bermuda and the north-east coast of North America with the comparatively sparse recoveries in Europe. Studies of plastic drift show that the North Atlantic current flow is mainly directed towards the western coasts of Ireland, western Scotland and south-west Britain. We have restricted most of our records to these regions, in particular to the Atlantic coasts of Ireland. While some disseminules from sub-tropical to tropical habitats, have been shown to be viable on arrival they may not survive as most do not reach suitable habitats, although some have germinated under managed conditions. The majority of the species reported as drift most probably arrive naturally but do not produce mature plant populations in Europe. Some strandings are likely to have human involvement. The ethnographic significance of some stranded disseminules suggests that these events have taken place over centuries and most probably throughout the Holocene. The increase of records of disseminules on European coasts in recent decades is likely to be due to more numerous interested observers with access to taxonomic guides and on-line information.

Highlights

- The behaviour of disseminules may closely follow that of floating plastics within the North Atlantic Ocean.
- Transmission of disseminules from the Americas to European Atlantic coasts range from 12° N to the Canadian east coast based on the distribution of parent plants. A greater latitudinal range is likely to be involved.
- The largest number of drift disseminule taxa arriving in Atlantic Europe and Macronesia belong to Fabaceae and Convolvulaceae.
- Small seeds may have more rapid crossing times but may be subject to greater losses from biofouling and sink on account of their surface to volume ratios. Many small seeds stranded on European shores have yet to be identified.
- Disseminules of different sizes are likely to have different oceanic routes and transit times according to varying current and meteorological conditions.

Keywords: Fruits, Ireland, natural spread, plastic, refuse, seeds, shore strandings, viability

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Introduction

Biota have been dispersed by ocean currents across deep water over geological time. Some of these will most probably have been with natural floating rafts (Van Duzer 2004). This includes the long-distance dispersal (LDD) of terrestrial vertebrates (Houle 1998); some crossings, for example of reptiles, have been deduced by using molecular hindcasting methods (Vidal et al. 2008). However, this hypothesis has not always received support (Mazza et al. 2019). LDD of marine biota is more plausible as indicated by recent studies of associations with floating algae (Rothäusler et al. 2012), or pumice (Bryan et al. 2012). It has been inferred using molecular techniques that during the pre-Pleistocene to early Holocene period, *Ostrea chilensis* Küster, 1844, that has a short planktotrophic period, rafted across the South Pacific Ocean from New Zealand to Chile, >7000 km (Ó'Foighil et al. 1999). Modelling has also shown that the distribution of some *Cycas* species within the Indo-Pacific region can be related to large-scale surface current movements (Liu et al. 2021). There are recent examples of invertebrates associated with floating plastics (Gregory 2009, Goldstein et al. 2014, Póvoa et al., 2021, De-la-Torre et al. 2023). Marine invertebrates of American origin attached to plastics have arrived on Irish and British shores (Holmes et al. 2015a), the same shores where open ocean neustonic invertebrate species have also become stranded (Minchin 1996; Headlam et al. 2020). LDD can also arise following volcanic (Bryan et al. 2012) and tsunami events (Murray et al. 2018).

For plants, depending on the size of the propagules involved, aerial transport (Muňoz et al. 2004), bird dispersal (Viana et al. 2016), and ocean transport (Gunn and Dennis 1999), are possible. The unfamiliar drift seeds collected from Orkney and western Scotland, were recognized as being the same as what Sloane (1698) had observed in Jamaica. He was the first to propose these might be carried across the North Atlantic by wind and ocean currents. Subsequently, further accounts of strandings from over a wider region within the northeastern Atlantic followed (in Nelson 2000). It was Darwin who undertook sea-salting experiments using the seeds of native plants that were floated in salt-water to test whether seeds could subsequently germinate to explain why some species occurred over ocean divides (Veak 2003). Later the widely travelled Guppy (1917) recorded strandings of disseminules in northwest Europe recognizing that these were of a Caribbean origin providing additional evidence of a link between these two regions. Colgan (1919) recorded tropical seeds from Irish shores. Later Ridley (1930) further developed the hypothesis to explain the biogeography of some plants. Since then, further disseminules were collected on European shores leading to the more complete account of Nelson (2000) of more than fifty taxa, not all of which could be considered to have arrived entirely by natural means. LDD can account for pan-tropical species, for example the coastal dune morning glory *Ipomoea pes-caprae* (L.) R.Br. (Miryeganeh et al. 2014). Many genera with floating disseminules have been recorded from the shores of Japan (Nakanishi 1987; Longhorn 2004; Vatanparast 2011), the Galapagos archipelago (Hamann 1984), India (Rajabudeen and Natarajan 2012), the South China seas and Australasia (Smith 1990, 1991, 1992, 1994, 2005; Smith et al. 1990), the Indian Ocean and South Africa (Muir 1933, 1937). Similarly records exist for the North Atlantic Ocean (Gunn & Dennis 1999; Perry & Dennis 2010; Nelson 2000), with records in the northeast Atlantic from Svalbard and Novaya Zemlya in the Arctic (in Nelson 2000) south to the Azores (Guppy 1917) and Macaronesia (Cadée & Dijksen 1999; Nelson 2002), a range of 48° latitude (77° N to 29° N). Greater numbers of disseminules and taxa have been recovered from a mid-region within this range: the Scottish Hebrides (Nelson 2000), Ireland (Colgan 1919; Nelson 1978, 2000) and southwest Britain (Gainey et al. 2020) the majority having an American origin.

Disseminule transmission by ocean currents requires buoyancy lasting from months to years. Buoyancy will depend upon cavities within the fruit or seed, lightweight cotyledonary tissue or fibrous outer coatings, as well as having an impermeable testa (Gunn and Dennis 1999). Disseminules stranding on European coasts originate from tropical and subtropical regions as well as temperate environments. Early accounts of disseminules in Europe include ethnological accounts and drawings before the parent plants and their geographical origin were fully known (in Nelson 1978, 2000). The stranding of unfamiliar seeds, on southern European shores during the fifteenth and sixteenth centuries provided evidence of the likely existence of an unknown land to the west, possibly the Spice Islands. Following colonisation of the Americas, American plants were imported to European gardens and the parent species of the stranded seeds and fruits were subsequently described.

Not all disseminules stranded on ocean beaches will have arrived by natural means. It is seldom possible to distinguish between truly peregrine (naturally spread) disseminules, and those subject to some human involvement, termed by Nelson (1978) as 'refuse' to refer to those having been disposed of, washed off a vessel's deck or perhaps from wreckage. Some will be involved directly or indirectly in commercial activities, for example, associated with timber imports/exports, for food, for processing into medicinal products, jewelry or curiosities, or by being available for purchase or exchange via the internet.

The duration of transmission within the North Atlantic will depend upon the course each disseminule takes and on wind and ocean current strengths and directions. Guppy (1917) indicated a need for a minimum floating capability of 14 months for an Atlantic crossing, although recent evidence suggests this may be less (Minchin 2021).

Colgan (1919) and Nelson (1978) provided records of strandings dating back to the late seventeenth century for Ireland: for a more complete account for Ireland and Britain see Nelson 2000; Jarzembowski & Jarzembowski 2014; Gainey 2020. Recent additions to the catalogue of species recorded on beaches in northwestern Europe since that of Nelson (2000) are provided by Quigley and Gainey (2014, 2018), Quigley and McNamara (2020), Quigley et al. (2020a, 2020b; 2020c) and Minchin et al. (2023).

We attempt to explain the paucity in the frequency and numbers of disseminule taxa stranded in Europe when compared with the North American east coast and Bermuda. We examine likely sources of entry, dispersal and fate while in transmission and the ranges of parent plants. Their dispersal is examined by comparing recent studies on the behaviour of plastics within the North Atlantic.

Materials & Methods

Disseminule sources of information

European and Macaronesia (here now including the Azores) records were sourced from records of Cadée (1997), Cadée and Cadée (2011), Cadée and Dijksen (1999), Colgan (1919), Gainey (2014; 2020), Hewitt (2012) Hood (2005), Jarzembowski and Jarzembowski (2014), Jonsell (2000), Minchin (1996; 2021), Minchin et al. (2023), Nelson (1978; 1990; 2002), Quigley and Gainey (2014: 2020), Quigley and MacNamara (2020,) Quigley et al. (2020a; 2020b), Rees (2019), Sjögren (1973), Thiel and Gutow (2005), and those reviewed within Nelson (2000). Collections of Irish material were identified, where possible to species, using Gunn and Dennis (1999), Nelson (2000) and Perry and Dennis (2010). Identifications of some retained species, or of photographs, were confirmed by Dan Austin, Charles Nelson and Ed Perry. For disseminules not determined to species, the generic name was used.

In Ireland disseminules were retrieved from shores within six regions. Four of these are exposed to the Atlantic and lie between the Islay front in the north (between Melmore Head, Co. Donegal, to the west coast of Islay, SW Scotland) and the Celtic Sea front (from the Saltee Islands off the coast of Co. Wexford to Hartland Point, Devon) as defined by Nichols (1898-1901) and supported by Simpson (1981) (Fig. 1).

While all Atlantic coastal regions were examined, not all were visited with the same frequency over the period 1982 to March 2023, covering all seasons; but not for all years. Searches were made on sand and shingle beaches and seaward shores of some estuaries. Some disseminules were recovered following storms within low-lying fields, behind fore-dunes and on clifftops. Tidal pools and lagoons, occasionally inundated during storms, also provided samples. Rarely were disseminules collected while floating in the sea. Private collections held by Quigley are included together with material freely provided by biologists (that appear in acknowledgements).

Records from North America and Bermuda were sourced from: Beerensson (2010), Dennis (1997), Ebbesmeyer (2006), Gunn (1968), Gunn and Dennis (1999), Guppy (1917), Kubitzki and Ziburski (1994), Nelson (2006), Norton (2007), Patterson (2001); Perry and Dennis (2010), Renner (2004), Spalding (2013), Sullivan and Williams (2007), Zies (1997; 2001) and from the on-line journal *the Drifting Seed* (http://www.seabean.com, for years 1995-2015).

The natural, latitudinal distribution of parent plants, and nomenclatural authorities for binomials, were obtained using online databases such as Plants of the World online (POWO), maintained by the Royal Botanic Gardens, Kew, UK (https://powo.science.kew.org/).

Geographic divisions used

Disseminules recorded from western Europe were divided according to five regions (Fig. 2). These regions

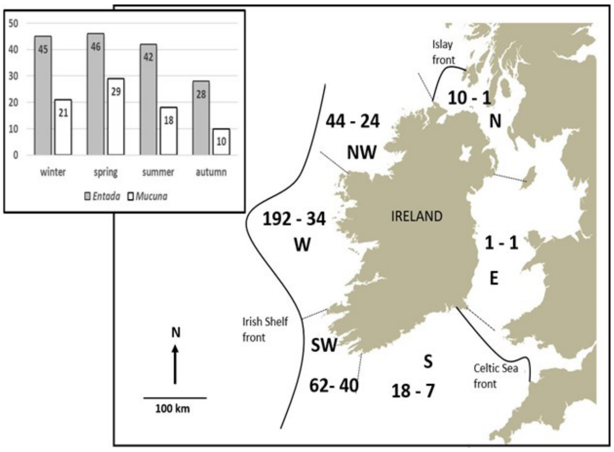

Figure 1. Six regions around the Irish coast where disseminules have been recorded in the literature and available to us from private collections. The total number of records of *Entada gigas* (to left) and *Mucuna* spp (on right) by area until the end of March 2023. Inset: Seasonal numbers of recorded collections of *E. gigas* (grey bars) and *Mucuna* spp. (white bars).

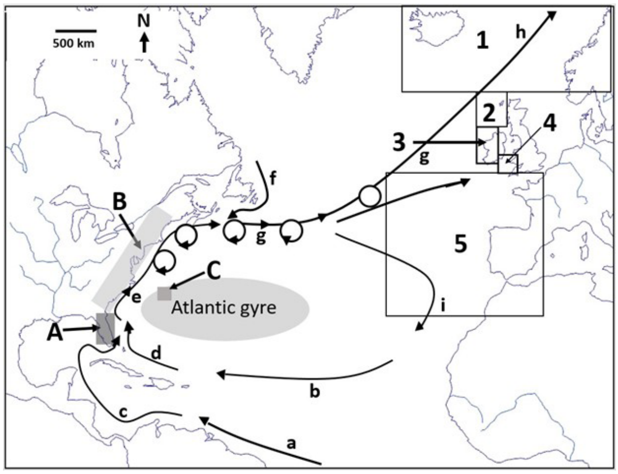

Figure 2. Regions where disseminules are known to have been stranded A: Florida, B: East North America, C: Bermuda shores. Receptor regions 1: Arctic region, 2: West Scotland, 3: Ireland, 4: SW Britain, 5: Continental Atlantic Europe and Macaronesia. Principal ocean currents a: Guyana Current, b: North Equatorial Current, c: Caribbean Current, d: Antilles Current, e: Gulf Stream and current rings, f: Labrador Current, g: North Atlantic Drift and current rings, h: Norwegian Current, i: Canary Current.

were from Atlantic coasts of western Scotland (2), Ireland (3) and south-west Britain (4). Records from European regions are based primarily on published accounts and findings from Ireland not previously reported. Additional geographic information, north of Scotland extends to Arctic seas (1), and from northern continental Europe southwards to Macaronesia (5).

European records of disseminules were compared with the extensive records of strandings on the coasts of Florida (A) and with records from the North American east coast (B) and Bermuda (C) (Fig. 2). Florida has an extensive set of accumulated records of stranded disseminules over decades (Gunn 1968; Gunn and Dennis 1999; Perry and Dennis 2010; and reported in *the Drifting Seed* (1995-2015). While some plant propagules stranded in Florida are from this region, many originate from areas to the south that may include northern South America. We used these records to compare with those recorded in the northeast Atlantic regions (1-5) (Fig. 2).

Species stranded on European shores and not recorded from shores within the Americas areas A to C were not considered. Nevertheless, disseminules purported to have an American origin in Nelson (2000), Skarpaas and Stabbetorp (2001), Thiel and Gutow (2005) and Rees (2019) have been included. The species stranded in regions A to C provide a basis for what might have been dispersed along the oceanic pathway to Europe.

Floatation experiments of disseminules

Floatation experiments undertaken by Gunn & Dennis (1999) and Perry & Dennis (2010) were based on disseminules that continued to float in still, salt water in receptacles. Some disseminules failed to float, whereas others remained afloat for months or years, in some cases many years. We use these results as an indication of the capacity of propagules to survive extensive oceanic transmission under a wide range of sea surface conditions.

Classification of drift disseminule transmission

We have no 'direct' evidence of disseminules having arrived naturally from the Americas, as these could not be followed throughout their journeys, nor do we have an indication of the tracks these undertook. The observation of arrivals in the eastern North Atlantic of species that occur naturally, or are introduced aliens (including those in cultivation) from the Americas, have in our classification three options. Accordingly, an appearance due to being: 'likely' based on duration of buoyancy and frequency and extent of records over decades; 'possible' where dispersal could theoretically take place based on floatation experiments; and where the level of certainty is lower due to the paucity of records and lower known capacity of floatation, or other evidence, and 'unlikely' where the natural transmission capacity is not convincing.

Sources of data for plastic drift and classification of ocean surface layers

We refer to the particle tracking reported by Bosi et al. (2021) for surface plastic movements in their North Atlantic study and the pathways that plastics can take. Drogues deployed during the 1990s provide current speed and general surface movements within the North Atlantic (Fratantoni 2001). For the low latitude circulation, we refer to Fratantoni et al. (2000). Current rings in the North Atlantic are complex transient features that include surface patterns that can be followed by satellite as shown in the studies undertaken by Leterme & Pingree (2008).

We use the surface zones that plastics occupy that are grouped according to plastic size with micro- (< 5 mm), meso- (5-25 mm) and macro- (> 25 mm) according to Hinata et al. (2017). Since plastics are usually buoyant, as are ocean dispersed disseminules, we use these same zones which are subject to different levels of movement in accordance with Stokes drift: '…*the net drift that a particle moving in a fluid's wave field*…' (Van den Bremer & Breivik 2017).

Measurements of stranded disseminules

Vernier calipers were used for measurements of globose species, using the maximum measurement and for discoidal or teardrop shaped disseminules for maximum measurement and diameter recorded down to the nearest 0.1mm using representative taxa. These measurements were used to classify their likely zone within the surface waters layers under calm conditions (Hinata et al. 2017). For the discoidal seeds of *Entada gigas* (L.) Fawc. & Rendle, *Mucuna* spp and *Macropsychanthus comosus* (G.H.Mey.) L.P.Queiroz & Snak the minimum measurements in the horizontal plane were also used, as the orientation of these within the water column can vary.

Sources of information for initial dispersal

We examined metrological events (NOAA 2020, 2021) that could lead to disseminules becoming displaced and entering the marine environment and then subsequently spread by wind over the ocean. This includes the vulnerability to hurricanes on the North American east coast (Cutter et al. 2007) and Caribbean region (Cambers 2009).

This account includes all studies known to us of strandings that have arrived in European waters based on previous historical accounts and attempts to explain the relatively smaller number of stranded disseminules collected on European shores when compared with that of the North American Atlantic coast and Bermuda. We speculate on the reasons in delays and paucity of disseminules arriving to European coasts.

Results

Native American plant species, and those introduced and established in the Americas that also have buoyant disseminules, have been recorded on European shores over a wide geographic range (Supplementary Table S1). Of the recovered disseminules recorded from European and Macaronesian shores we consider that twenty-eight are likely to have undertaken an ocean transmission from the Americas and fifteen may have possibly undertaken such a journey. The families most frequently represented are Fabaceae and Convolvulaceae, with twelve (eleven species, one genus) and six (five species, one genus) taxa respectively, that are likely, or may have possibly, made such an ocean journey without human interaction (Fig. 3). These two families have the greatest north-south range and contain both temperate, sub-tropical and tropical species. Juglandaceae is represented by six species. Arecaceae (Palmae) is represented by six taxa (four species and two genera). The families of Lecythidaceae and Euphorbiaceae each have two representative species. Nine families are represented by a single species and includes two genera for the Meliaceae. All families (in Supplementary Table S1) have a range that extends within or throughout the storm/hurricane zone (Fig. 4). We have assessed the following *Cassia fistula* L., *Delonix regia* (Bojer ex Hook) Raf., *Mangifera indica* L., *Nypa fruticans* Wurmb and *Swietenia* Jacq. as being unlikely to undertake a natural ocean crossing on the basis of their poor ability for extended floatation, although records of strandings exist. This may include some species of *Calophyllum* L. (Quigley et al. 2023). One of these, *Manilkara zapota* (L.) P.Royen, has a range solely within the northern hemisphere (Supplementary Table S1).

The most commonly recorded species throughout the European and Macronesian regions have been *Mucuna sloanei* Fawc. & Rendle, *M. urens* (L.) Medik. and *Entada gigas* (L.) Fawc. & Rendle, conspicuous on beaches on account of their size and form. These species along with *Guilandina bonduc* L. (syn. *Caesalpinia bonduc* (L.) Roxb.) have been shown to be viable once stranded (Nelson 1990, J. Hassett pers com., DM pers ob.). Smaller disseminules are generally recorded less frequently, for example *Canavalia* spp., except where the small seeds are stranded in large numbers or have been specifically sought, such as *Lathyrus japonicus* Willd. var. *maritimus* (L.) J.T.Kartesz & Gandhi (Minchin 2021).

The majority of recorded disseminules remain afloat for 12 or more months, six species having shorter floatation times than this. Some, present on shores on both sides of the Atlantic with an estimated maximum three-months buoyancy, are most unlikely to survive an Atlantic crossing, for example, *Mangifera indica* L.. Species with buoyancy estimates of more than a hundred months include members of Fabaceae and Convolvulaceae that are frequently recorded within European regions (Supplementary Table S1).

Disseminules carried in oceanic currents vary in size. Their dimensions fit within, and overlap, the surface ocean layer zones as defined for plastics by Hinata et al. (2017). Different genera, according to their size, occupy different zones. Some of the smallest disseminules, from Fabaceae and Convolvulaceae, are predicted to occupy the micro-zone, whereas larger disseminules, including larger seeds of Fabaceae, may extend more than 25 mm from the surface according to their orientation (Fig. 5).

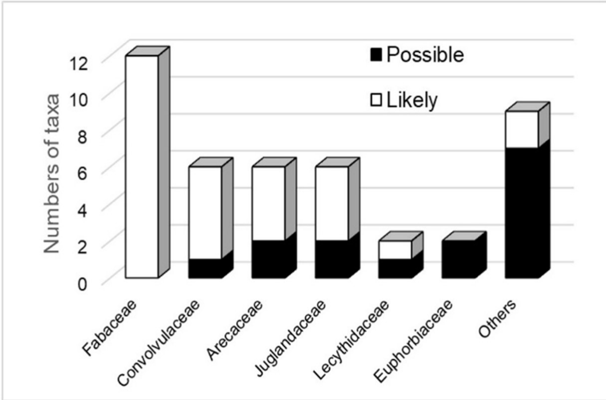

Figure 3. Numbers of stranded taxa by family recorded from northeast Atlantic shores likely to have been naturally transmitted (white). Families with taxa that possibly endured an oceanic crossing (black).

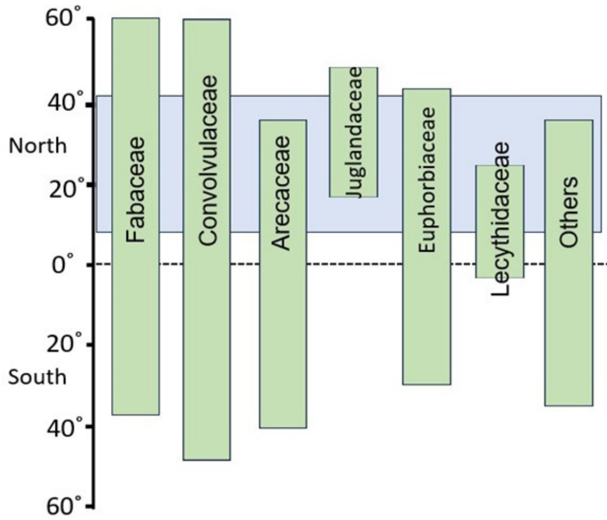

Figure 4. Latitudinal ranges of the main families (green) with taxa in this study, with floating disseminules likely to have crossed the North Atlantic. General range of seasonal storms/hurricanes within the Americas on the Atlantic coast (blue). Data based on POWO 2023.

Discussion

The spread of floating plant propagules within the North Atlantic must have occurred over geological time. Yet there is evidence that spread by surface drift can take place over shorter periods. The emergence of the volcanic island of Surtsey in 1963, to the south of Iceland, lead to several shoreline plants becoming established within a four-year period (Friðriksson and Johnsen 1968). One of these, *Mertensia maritima* (L.) Gray, has seeds that float in sea-water and can germinate following stranding (Skarpaas and Stabbetorp, 2001) and is a circum-polar species (POWO 2023). While the crossing of the Atlantic has involved some temperate disseminules that float, the majority

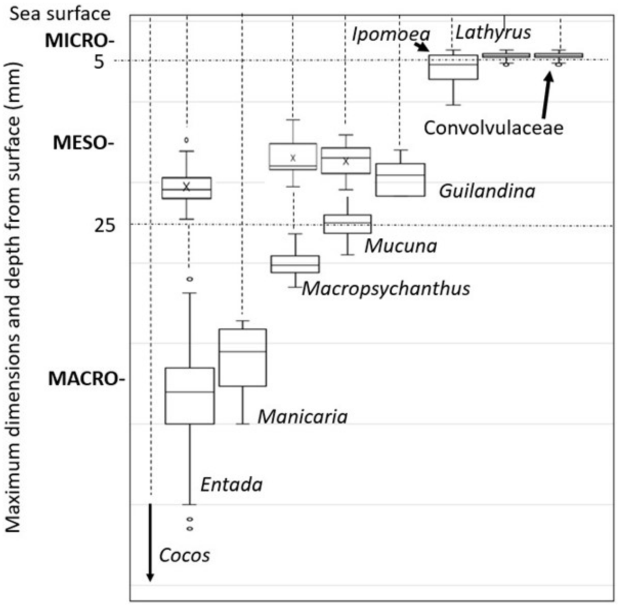

Figure 5. Surface water zones and relative maximum dimensions of some disseminules (with standard deviations and ranges) for the maximum extent occupied from the surface according to the classification of different zones (in mm) occupied by different sizes of drifting plastic (after Hinata et al. 2017). The orientation of some discoidal species can vary, those normally positioned horizontally in the water are indicated with 'x'. Disseminules exceeding these measurements most probably sink. See also below for what can modify the zones of occupation.

recorded will have arrived in northwest Europe from sub-tropical to tropical environments.

Disseminules from the Americas, arriving in European regions, are not always viable, as within the Arecaceae (Nelson 2000, Perry and Dennis 2010). In many cases this is due to damage to the endosperm, yet the fibrous mesocarp can maintain buoyancy. In the case of *Cocos nucifera* L*.,* while most often buoyant, with part of the drupe exposed above the surface, not all are capable of maintaining floatation as there are records of specimens recovered from dredge samples (Gunn and Dennis 1999) and two from the Porcupine Bank taken in trawls about 240 km off the west coast of Ireland (DTGQ). Not every disseminule of a stranded species can float; of eight intact *Manicaria saccifera* Gaertn. Endocarps, recently stranded on a Florida beach, three sank (DM pers ob.). Perry and Dennis (2010) record that a single mesocarp of this palm floated for 30 years and while *Cocos nucifera* drupes can remain viable for 110 days in sea-water (in Beveridge 2022), whereas the mesocarp can remain afloat for up to thirty years (Perry and Dennis 2010). Consequently, part of the fruit is capable of an oceanic transmission. The finding of a germinating *C. nucifera* on an Irish western beach during January 1987 (M. Viney pers. comm.), with an intact unfouled exocarp, would suggest a human involvement. Disseminules found on shores that did not re-float, may have arrived by some other means or sank while close to shore.

There is no doubt many American disseminules from tropical to temperate habitats have been carried within North Atlantic currents to isolated islands and western Europe. We consider that many of these were likely to have undertaken this journey as a result of natural dispersal. The parent plants occur at, or near to, coasts. For those species that only occur naturally inland, the disseminules most probably were carried by rivers to the coast and subsequently dispersed by oceanic currents.

While we recognize that disseminules may also have been carried in part by human movements for different purposes, or result from unintended losses, we contend that the greater number have arrived naturally over long periods of time. We also consider that many small disseminules, not generally noticed on shores and with many yet to be identified, also have spread naturally. Most of these belong to the genera Fabaceae and Convolvulaceae.

Bosi *et al.* (2021) used particle tracking models to calculate that North Atlantic currents direct the main volume of plastic particles towards the north of Ireland at 55° N, with extensive beaching within ten degrees to the south and 15 degrees to the north (Fig. 6). The north of Ireland also coincides with the simulated destination based on oceanic drifter datasets (Rypina et al. 2011). The majority of disseminule records from European coasts have also been from the same regions 2 to 4. We used this model to evaluate a comparable behaviour of disseminules, which share similar depth zones and circumstances such as sinking from biofouling, possible damage and ingestion and transmission by vertebrates. All shore collections clearly indicate a wide biogeographical origin. Irish Atlantic shores are often associated with drift materials from the Western Atlantic, for example, Canadian and American milk product cartons, light sticks used in offshore fisheries and North American lobster trap floats that are reused in Ireland (Fig. 7). While few can be certain as having a specific origin, some tags from various North American fisheries can be related to a provincial region (Minchin 2021).

We now examine the parent ranges of disseminules that subsequently appear in the western North Atlantic along with distances involved and the fate that may become them on such journeys.

Biogeographical ranges of parent plants

We used the appearance of disseminules stranded on the coasts of Florida, Bermuda and eastern North America as representing taxa whose geographical ranges may have been extended naturally to Atlantic European and Macaronesian shores by ocean currents and by wind. Collections from this region have been made over decades (Gunn and Dennis, 1999; Perry and Dennis 2010 and in the *Drifting Seed* 1995-2015) Some of the disseminules will have an origin to the south of Florida from tropical environments; but apart from occurring from within their parent plant range we are unable to otherwise indicate a source. Some have natural ranges to the north of Florida and Bermuda being indigenous in temperate habitats in

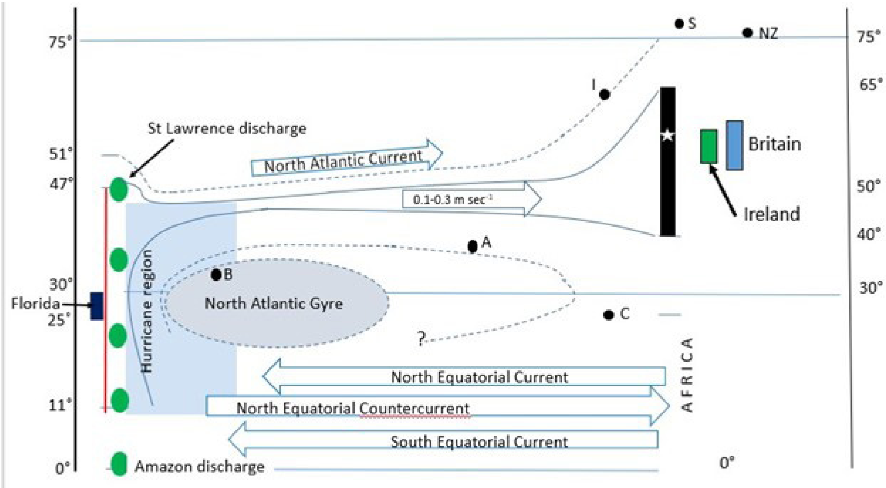

Figure 6. Diagrammatic representation of the North Atlantic showing likely sources of disseminules from temperate to tropical regions (red bar) and a contribution from possible river discharges (green ovals). The main reference point Florida (dark blue bar) with B (Bermuda) and the region of seasonal storms during June to November (pale blue). Termination range of plastics in Europe (black bar) with principal destination region of plastics (star) and of records from regions 2 for Scotland and 4 SW Britain (blue) and for Ireland (green). Receptor islands I (Iceland), S (Svalbard), NZ (Novaya Zemlya) with A (Azores) and C (Canaries) representing Macaronesia. Blue lines indicate principal routes of plastics and dashed lines most probable range of disseminules. Degrees are of latitude.

Figure 7. Clockwise: *Macropsychanthus comosus* (G.H.Mey) L.P.Queiroz & Snak with a small colony of *Lepas pectinata* Spengler, 1793. *Dosima fascicularis* (Ellis & Solander, 1786) with its naturally produced float attached to a seed of *Lathyrus japonicus* var. *maritimus*. Floats, used in the North American lobster fishery, in reuse in an Irish fishery. Extensive stranding of floating marine algae *Sargassum* spp., originating from the North Atlantic Gyre, on an east facing shore on Martinique, Windward Islands. (Photos: D. Minchin)

eastern North America. An example is the sea pea, *Lathyrus japonicus* var. *maritimus,* that is native in north-eastern North America and is considered to be a native species in Ireland, Britain and north-western Europe. The western and south coast Irish populations of this pea are most likely to have arisen from seeds dispersed from temperate North America (Nelson 1986, Walsh & Nelson 1987, Minchin 2021). *Calystegia sepium* (L.) R.Br. is also almost certainly involved in similar transmissions (Nelson 2000; Rees 2019). There are six subspecies of *C. sepium* occurring in North America. This includes a subspecies that occurs naturally in Europe and that has been introduced to North America (Spalding 2013). A genetic study is needed to reveal the geographical affinities of European shoreline populations of such subspecies.

Disseminules are sourced from the latitudinal range of parent plants (Supplementary Table 1), or from re-floating of stranded seeds. The majority of parent species do not grow naturally north of 25° N, but it is unclear how far south we can prescribe an origin, although some disseminules probably have their origin in the Amazon Basin entering the coast at the Equator (Fig. 6). As judged by the study of ocean drifters (Limeburner et al. 1995) disseminules disgorged from the Amazon may be carried in the Guyana, Caribbean and Antilles currents towards the Gulf Stream (Fig. 2). Disseminules of species of *Astrocaryum*, *Mucuna* and *Erythrina*, as well as *Omphalea diandra* L. and *Caryocar glabrum* (Aubl.) Pers., have been collected floating in the Amazon River (Zies 2001). Although these have geographical ranges that extend into northern latitudes, some, such as the native range of *Sacoglottis amazonica*, extend northwards from the Amazonian Basin to 12˚ N (POWO 2023). There is almost certainly a contribution from other American rivers that include the Essequibo (Guyana), Orinoco (Venezuela), Magdalena (Colombia), Rio Grande (Mexico) and the Mississippi and St Lawrence rivers (United States of America and Canada). Smaller rivers on islands may also make contributions, for example, the vine *Entada gigas* occurs in inland semi-tropical rain-forests on the larger islands of the Caribbean (Kelly 1985); and in Central and northern South America with a latitudinal range of 12˚ to 22˚ N (POWO 2023). We are unable to suggest that plants found naturally south from the Amazonian discharge to Argentina, or having an African origin, are involved in European strandings. However, Kistler et al (2014) have shown, using genetic methods, that the African bottle gourd (*Lagenaria siceraria* (Molina) Standl.) most probably arrived in the Americas as drift from Western Africa. This took place about 10,000 BP. Using drift simulation models, they estimated this crossing took less than a year.

Distances involved in transmissions

While most disseminules are sourced from the east coast of the Americas some may have an African origin (Kistler et al. 2014). Renner (2004) provided evidence that disseminules of some palm species (Arecaceae), having been transferred within the South Atlantic Equatorial Current to the western Atlantic, then transferred northwards to the Guyana current and beyond (see Fig. 2).

The stranding of *Ipomoea alba* L., *Macropsychanthus comosus* (syn. *Dioclea reflexa* Hook.f.) *Mucuna sloanei* and *Entada gigas* in Lanzarote (Cadée and Dijksen 1999), *Acrocomia* sp. in Tenerife (Cadée and Cadée 2011), and of *E. gigas, Guilandina bonduc, M. comosus* and *Mucuna sloanei* (Hood 2005) on Porto Santo (close to Madeira) (and most probably a stranding of *Lathyrus japonicus*, found as a single plant on the high shore in the Azores (Sjörgren 1973)) all suggest a transmission across the North Atlantic and subsequently via the Canaries Current. While there is no evidence of a continued drift of disseminules into the North Atlantic Gyre, this possibility exists for disseminules capable of remaining afloat for some years. Under experimental conditions, some disseminules have remained afloat for more than thirty years (Perry and Dennis 2010). Within this gyre plastics also collect and appear mainly within 0.5 m of the surface (Reisser et al. 2015) with a long residency (Bosi et al. 2021). As several tropical and sub-tropical disseminules have been recovered from the shores of Bermuda (Patterson 2001), there is also the possibility disseminules may enter this gyre earlier from the Gulf Stream. This gyre is a region where holopelagic *Sargassum* spp also collect in abundance. On occasions, large amounts *Sargassum* accumulate on exposed Caribbean shores (Bartlett and Elmer 2021) and these accumulations may contain long-distance diseminules (Fig. 7).

Seeds from temperate habitats in North America, such as those of *Lathyrus japonicus* var. *maritimus*, have to travel at least 4,000 km to reach Ireland, whereas those from Florida have approximately 6,500 km and from the Brazilian Amazon have a journey of about 16,000 km. This does not take into account displacement on such a journey within current gyres. The longer distances may incur higher losses through loss of buoyancy, or by becoming stranded on nearer shores. Some of these might become re-floated to continue their spread.

Peregrine and 'refuse' disseminules

Disseminules recorded from the North American regions A, B and C have a potential to reach Europe and transmissions for a proportion of these are polyvectic. While we are uncertain each collected specimen was spread by natural means from a natural source, the bulk of specimens are most probably peregrine since these had a widespread occurrence on European shores with accounts extending over a century (in Nelson 2000). The Irish collections, made over several decades, are more likely to represent peregrine disseminules as these can be associated with North American flotsam occurring on exposed Atlantic shores. The smaller, seldom recovered seeds are likely to be peregrine being normally overlooked and are most likely to be under-recorded.

'Refuse', a term used by Nelson (1978, 2000), refers to disseminules involving some human involvement. These are normally recorded as localised accumulations or rare finds (for example, *Ricinus communis* L., *Manilkara zapota* (L.) P.Royen, *Myristica fragrans* Houtt. (Guppy 1917; Cadée 1997; Nelson 2000)). Some 'refuse' species have been shown to have poor or no buoyancy or with very few individuals capable of floating (Nelson 2000). Some of these, such as *Mangifera indica* L., have fleshy fruits and are considered unlikely to be naturally dispersed by ocean currents as these are more likely to have evolved for terrestrial animal dispersal (Esteves et al. 2015). Others demonstrate a clear human involvement, for example, the decorated coconuts (*Cocos nucifera*) released during Hindu festivals in Britain (Hewitt 2012). This palm, perhaps originating in the Pacific region (Beveridge et al. 2022), has been spread by humans and has colonised many tropical oceanic islands, and does have a limited capability of germinating following dispersal in currents. However, most coconuts, but not all, from Irish beaches that have been immature fruits or have had surface and boring biota may have undertaken a prolonged oceanic journey (Nelson 1978; Minchin pers ob.).

Hydrochory, how it begins

Most parent plants have coastal distributions that overlap the 'hurricane belt', a region that generally occurs between 10° N and 43° N. The intensity, frequency and tracks of hurricanes within this 'belt' vary with a season, normally from June to November; but mainly August to October (NOAA 2020, 2021). These events can remodel beaches through the effects of tidal surges, strong winds and extensive rainfall (Sallenger et al. 2006). The stripping of fruits from parent plants by wind can also result in disseminules entering the sea. Following such events, large strandings, including these species, can occur on shores in Florida (Perry & Dennis 2010). Storms can damage fore-dunes, yet plants in such regions can be adapted to such events and be capable of recolonization from ocean-dispersed propagules. An example is *Ipomoea pes-caprae* which has a pan-tropical distribution and seeds well adapted for ocean travel (Davy and Figueroa 1993). Other strandline plants such as *Guilandina bonduc* (30° N - 18° S) and *Canavalia rosea* (Sw.) DC (30˚ N to 32˚ N) have similar capabilities (Mendoza-González et al. 2014).

On entering coastal waters, the surface water movements are determined by wind and current speed and direction, and flotsam may subsequently enter looping eddies (Richardson 2005). Some of the disseminules might become carried by the Caribbean Current, or perhaps the Antilles Current, to enter the Gulf Stream. In the Caribbean Sea and Gulf of Mexico disseminules are stranded in abundance on the shores of the Yucatán Peninsula (Gunn et al. 1984) and Costa Maya in Mexico (Ebbesmeyer 2006) and on beaches in Texas (Ebbesmeyer 2008; Sullivan 2004; Sullivan and Williams, 2007, 2008, 2010) including Padre Island (Norton 2007). Once off the east coast of Florida, after north-easterly storms, during October to May (Zies 1999), large accumulations of disseminules can appear on shores (Norton 2008). As noted, floating seeds also reach Bermuda (Patterson 2001). Flotsam is also carried further offshore along the coasts of the eastern North America as far north as Cape Hatteras (Ribic et al. 2010), with rare strandings further north on Sable Island off the Canadian coast (Nelson 2006) and Greenland (Gunn 1968).

Delays in transit

As the surface of the Gulf Stream flows northwards, temperate American plants, may become added to the flotsam and enter the North Atlantic Drift. Furthermore, seeds carried within the cold Labrador Current meet the Gulf Stream above the latitude of Cape Hatteras may also enter the North Atlantic Drift (Nelson 2000, Minchin 2021). The margins of the Gulf Stream and North Atlantic Drift form cold and warm-core meandering rings, with diameters normally exceeding 100 km (Auer 1987). There are variations in the size, number and duration between years, occurring at a greater frequency this century. These rings usually develop in the late spring to early summer (Gangopadhyay et al. 2019) and can entrap flotsam leading to a separation of former drift associates. The eastward flow of the North Atlantic Drift is exposed to predominantly westerly wind. When off the coast of Ireland this current broadens and extends northwards into the Norwegian Current to Norwegian coasts and the Arctic Sea and southwards within the Canaries Current to off the west coast of Africa, as we have discussed.

Losses in transit

Continued transmission of plant disseminules depends on continued floatation which can be impaired by the surface growth of fouling organisms such as lepadid cirripedes (Gunn and Dennis 1999; Fig. 7) and by boring biota (DTGQ; Holmes et al. 2015b). A heavy accumulation of these may eventually result in the disseminules sinking. An exception is the pelagic goose barnacle, *Dosima fascicularis* (Ellis & Solander, 1786) (syn. *Lepas fascicularis* Ellis & Solander, 1786) that normally attaches to small floating items. As the colony grows it produces a spongey float to compensate for its increased weight (Fig. 7). Apart from attaching to the ~5 mm seeds of *Lathyrus japonicus* it also attaches to small pieces of man-made substrates such as tar and plastic, where formerly it was mainly associated with feathers and pumice (Minchin 1996). The high surface to volume ratio of small disseminules must pose a disadvantage due to the risks from epibionts. For some, a loss of buoyancy from seepage of water through the micropyle, or damage to the testa, may result in sinking.

The extent of fouling may relate to prolonged periods at the surface. More rapid fouling may be expected in warmer waters. On entering cooler water currents epibionts may expire or their growth become retarded. Temperate seeds probably have the advantage of shorter journeys in cool water, with possible lower levels of fouling. While attached biota may result in sinking, albeit perhaps not all the way to the bottom, it is possible for plastics and disseminules to refloat once the attached biota disintegrates. Sinking is a real risk as disseminules have been dredged from deep-water sediments (in Gunn and Dennis 1999). This parallels the fate of plastic, with smaller plastic pellets (up to 5 mm) sinking sooner (Fazey and Ryan 2016). Despite the depletion of small plastic particles at the ocean surface, micro-plastic discoidal pellets, 'nurdles', reached Irish shores in abundance during the 1980s and 1990s (Nelson 2000: DM pers. ob.). Recently there has been a notable decline in 'nurdle' strandings (Van Franekar and Law 2015).

Disseminules can bear scars and bite marks. These can be inflicted soon after release from a parent plant. A *Mucuna* seed was seen falling into a South American river to be eaten by a pacu (a serrasalmid fish of which there are several similar species) (Perry 2000). Disseminules, of a wide range of species, in the Amazon Basin are avidly consumed by various fishes (Kubitzki & Ziburski 1994). Some may sustain damage to the testa in freshwater or after entering the sea. Examples of *Entada gigas, Guilandina bonduc, Mucuna* species and *Terminalia catappa* L. are reported showing similar upper and lower surface damage, indicative of vertebrate bite-marks that may be due to turtles (Beeresson 2010; Perry & Dennis 2010).

In the Pacific Ocean, *Macropsychanthus, Entada, Caesalpinia, Mucuna, Terminalia, Calophyllum* and *Balsamocarpon brevifolium* Clos (syn. *Sophora microphylla* Meyen) disseminules have been found in albatross nests, some within chick carcasses (Wagner 2002). An *Ipomoea* seed was reported in a giant petrel's nest on Macquarie Island, south of New Zealand at 54˚S (Smith 2006). Fulmars have long foraging ranges even when nesting (Edwards et al. 2013). However, there is less such evidence from the North Atlantic, although off the west coast of Scotland, at St Kilda, a seed of *Guilandina bonduc* was recovered from a fulmar's nest and some from the crops of other fulmars (in Nelson 2000). Fulmars, shearwaters and petrels feed on organisms at the water surface, and so may have acquired the disseminules targeting the associated fouling or perhaps the colour of the seed. Moore (2008) claimed plastics are mistaken for food by albatross, fulmars and shearwaters. While *Entada gigas* is too large for such North Atlantic birds to swallow or hold, smaller disseminules may be more vulnerable to ornithochory.

Much of the European Atlantic coastline has a rocky coast where arriving disseminules may become damaged or destroyed. Damaged *Entada gigas*, lacking endosperm, have been found on Irish shores (DM pers. ob.). It is unknown how many become destroyed in this way.

The case for selective dispersal

Disseminule size, buoyancy, degree of fouling and varying exposure to currents may explain the apparent spread in distance and time involved, and for the fewer records being stranded on European shores. This compares with the mainly seasonal large strandings in Florida that take place, often after storm events. According to Bosi et al. (2021) the surface levels in which plastics float are important for their rate of spread. This relates to the surface water profile involved in the differential rates of movement according to Stoke's drift. There are three depth zones from the surface, micro- (< 5 mm), meso- (5 – 25 mm) and macro- (> 25 mm), as defined by Hinata et al. (2017). There being a more rapid transmission for objects floating on or near the surface. These depth categories can broadly be related to the sizes of disseminules in this study (Fig. 5). Those in the micro-layer could include *Lathyrus japonicus* var. *maritimus* and many species of Convolvulaceae and so result in their swifter dispersal. During storms (≥ Beaufort scale 10) this surface zone may become stripped from wave-crests, with seeds having moments of aerial transport along with spume. Even during wind speeds of 14 m/s (Beaufort 7) the mean size of sea-water drops, about 6 mm diameter (Anguelova et al. 1999), may exceed the dimensions and density of the smallest seeds.

The micro- to meso- zone could account for the majority of disseminules arriving on European shores. Under wave conditions disseminules may tumble with momentary appearances within a different zone, perhaps circulating to some depth, depending upon their size and density. Plastics in high sea states may have periods of vertical circulation, and the surface rise velocity will result in different durations according to the separate surface layers occupied (Reisser et al. 2015). The mean wind speed from ocean buoys off the west coast of Ireland ranging from 3 to 6 m/s (Beaufort 2 to 4) (Blackledge et al. 2012). This makes tumbling and circulation of disseminules within different surface zones likely. Larger disseminules within the macro-classification could take longer in making an Atlantic crossing and so be more likely to carry cyptofauna, residing hidden within protective layers of the disseminule and surface growing epibionts.

Problems of recording

It is only in recent decades that records of disseminules have increased, with a likely bias towards larger disseminules, smaller seeds either being generally overlooked or of little interest. Visits to shores, during strong onshore winds, may not be productive due to extensive foam and/or burial from drifting sands. Frequently reported Irish finds are of *Entada gigas* and *Mucuna* spp. Yet many finds go unreported, being retained as keepsakes, sometimes to be later acknowledged as having been found (Fig. 1). In Ireland most of the strong wind conditions occur outside the summer and may explain the many finds during the winter and spring when there may be fewer recorders present on shores, indicating possible seasonal bias, yet with similar findings during the summer, when there is an increase in human activity on beaches. Some found in summer may have been stranded some months before. Almost certainly, the majority of stranded disseminules do not come to the attention of recorders. It appears that some beaches are more productive than others due to their orientation and tidal dynamics. Neilson and Costello (1999) estimated that 34% of the 7534 km of Irish coastline was made up of sand, involving only some of the most likely areas where collections would be made.

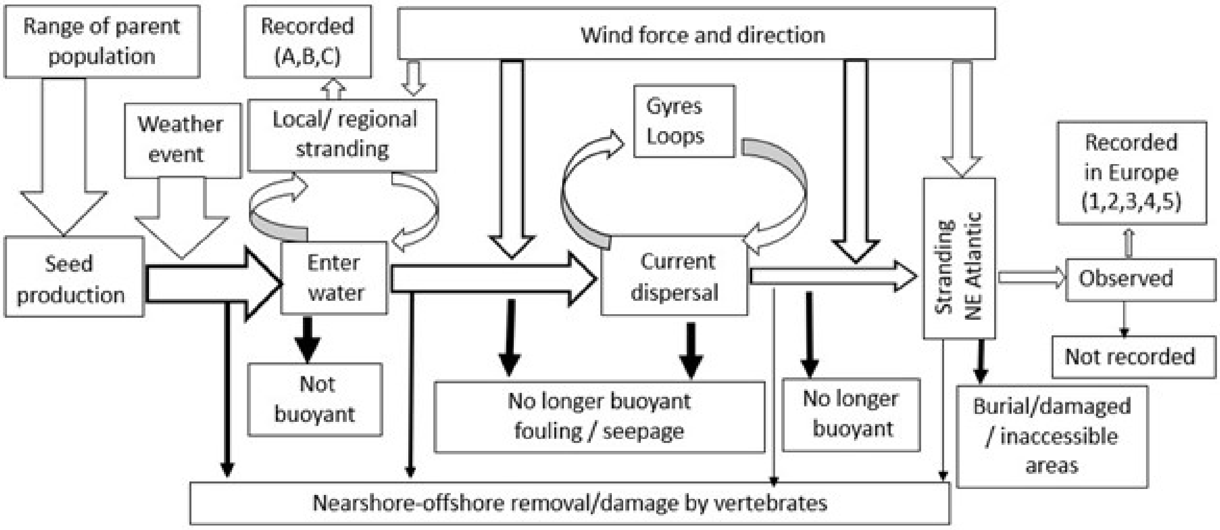

Figure 8. Risks for disseminules associated with oceanic travel from the Americas. Recording areas are described in Fig. 2.

Overall risks in transit

Disseminules capable of floating for a long period have been found at a greater frequency on subtropical and tropical shores often within the range of their parent plants (the *Drifting Seed* 1995-2015). Those capable of spreading northwards can accumulate in large numbers on Florida shores, usually following onshore winds and recent storm activity. The sparse records in Europe most probably relate to a comparatively low level of survival in oceanic transit from sinking, small number of recorders (Fig. 8) and being spread over a wide region from Arctic shores to Macronesian islands.

The buoyancy of many disseminules may not be secure due to fouling and absorption of water while in transmission (Fig. 8). Nevertheless, small propagules may undertake shorter crossing times due to the level at which they float in the water column, perhaps assisted, in part, by aerial transport. Vertebrates may cause losses during transit. The distances disseminules travel are uncertain as many parent plants have a wide latitudinal range. There is the possibility that journeys, for some, may start in western Africa, or, having crossed the Atlantic towards Europe, may become distributed southwards to the Canary Islands and so might subsequently enter the North Atlantic Gyre, especially those disseminules capable of buoyancy over many years.

Conclusions

Disseminules from temperate to tropical environments have been spread by oceanic currents over geological time with accounts of those from the Americas being recorded in European folklore to recent times. These have been found stranded from Svalbard and Novaya Zemlya within the Arctic circle south to the Macaronesian islands. Records of taxa from the Atlantic coasts of Scotland, Ireland and southwestern Britain have been the most numerous, involving twenty-eight taxa likely to be true peregrine species and with some small seeds yet to be identified. This region corresponds with the tracking of plastics across the North Atlantic to this same region. The most frequently observed taxa are from the families Fabaceae and Convolvulaceae, followed by Arecaceae and Juglandaceae. Generally, the spread of disseminules involves a polyvectic process that may include hydrochory from rivers and flooded wetlands, from seasonal rainfall and coastal areas following storm events to later becoming spread by ocean and wind currents, some with an often-unclear human involvement.

Disseminules, like plastics, can endure delays should they become stranded, to perhaps become refloated, or later enter wandering current rings during an oceanic transmission. Changes in current speed and wind force and direction will influence the duration of travel and according to the surface zone occupied that relates to disseminule size, shape and orientation and levels of fouling. Small plastics, on account of their high surface area to volume ratios, that will influence their buoyancy, may be more prone to sinking as may take place for some floating disseminule taxa.

There are considerable distances involved for the disseminules that arrive on European shores. American disseminules, with long floating times, might enter the North Atlantic Gyre, having passed close to Bermuda or via the North Atlantic Drift. There is the possibility that some circumnavigate the North Atlantic and those from west Africa may arrive via Equatorial currents to enter the North Atlantic.

There are further opportunities for the establishment of disseminules stranded in a viable state within the wide range of changing climatic destinations. The predicted increase in the intensity and number of storm events within the Americas may lead to greater numbers of disseminules being carried within ocean currents.

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Author Contributions

DM conceived the idea and wrote the account. DTGQ shared his knowledge of collections and reviewed drafts. Both authors declare that there were no ethical matters or conflicts of interest in relation to this study.

Supplemental Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb
Table S1. Trans-Atlantic disseminules recorded on European shores.

References

Anguelova, M., Barbar, R.P. & Wu, J. (1999) Spume drops by the wind tearing of waves. Journal of Physical Oceanography, 29, 1156-1165. https://doi.org/10.1175/1520-0485(1999)029<1156: SDPBTW>2.0.CO; 2

Auer, J.A. (1987) Five-year climatological survey of the Gulf Stream system and its rings. Journal of Geophysical Research, 93, 1709-11726. https://doi.org/10.1029/JC092iC11p11709

Bartlett, D. & Elmer, F. (2021) The Impact of *Sargassum* inundations on the Turks and Caicos Islands. Phycology, 1, 83–104. https://doi.org/10.3390/phycology1020007

Beerensson, J. (2010) Interaction between species. The Drifting Seed, 16, 5.

Beveridge, F.C., Kalaipandian, S., Yang, C. et al. (2022). Fruit biology of coconut (*Cocos nucifera* L.). Plants, 11, 3293. https://doi.org/10.3390/plants11233293

Blackledge, J., Coyle, E., McGuirk, R. et al. (2012) Analysis of wind velocity signals for estimating the wave power density of Ireland's coastal resource. IET Irish Signals and Systems Conference (ISSC 2012). Maynooth, Ireland 28-29 June 2012. https://doi. 10.1049/ic.2012.0176

Bosi, S., Broström, G. & Roquet, F. (2021) The role of Stokes drift in the dispersal of North Atlantic surface marine debris. Frontiers in Marine Science, 8, 697430. https://doi.org/10.3389/fmars.2021.697430

Bryan, S.E., Cook, A.G., Evans, J.P. et al. (2012) Rapid, long-distance dispersal by pumice rafting. PLoS ONE, **7**, e40583. https://doi.org/10.1371/journal.pone.0040583

Cadée, C.G. (1997) Tropical drift disseminules from the coast of the Netherlands: the human factor. The Drifting Seed, 3, 3-4.

Cadée, G.C. & Cadée, M.C. (2011) *Acrocomia* sp., a prickly palm seed from Tenerife (Canary Islands). The Drifting Seed, 17, 8-9.

Cadée, C.G. & Dijksen, S. (1999) *Mucuna* and *Dioclea* from Lanzarote. The Drifting Seed, 5, 12 - 13.

Cambers, G. (2009) Caribbean beach changes and climate change adaptation. Aquatic Ecosystem Health & Management, 12, 168-76. https://doi.org/10.1080/14634980902907987

Colgan, N. (1919) On the occurrence of tropical drift seeds on the Irish Atlantic coasts. Proceedings of the Royal Irish Academy, 35B, 29-54. https://www.jstor.org/stable/20517053

Cutter, S.L., Johnson, L.A., Finch, C. et al. (2007) The US hurricane coasts: increasingly vulnerable? Environment: Science and Policy for Sustainable Development, 49, 8-21 https://doi.org/10.3200/ENVT.49.7.8-21

Davy, A.J. & Figueroa, E. (1993) Colonisation of strandlines. In: Primary succession on land. (ed. By J Miles and DWH Walton), pp 113-131. Special Publication Number 12 of the British Ecological Society. Blackwell Scientific Publications, Oxford.

De-la-Torre G.E., Arribasplata, M.B., Roman, V.A, et al. (2023) Marine litter colonization: methodological challenges and recommendations. Frontiers in Marine Science, 2, 1070575. https://doi.org/10.3389/fmars.2023.1070575

Dennis, J.V. (1997) Stranded tropical disseminules from Cape Hatteras and nearby beaches in North Carolina, USA. The Drifting Seed, 3, 7.

Ebbesmeyer, D.C. (2006) Sea beans in hog heaven. The Drifting Seed, 12, 5-8.

Ebbesmeyer, D.C. (2008) On a flotsam collection beach: Matagorda Island, Texas. The Drifting Seed, 14, 12-14.

Edwards, E.W.J., Quinn L.R., Wakefield, E.D. et al. (2013) Tracking a northern fulmar from a Scottish nesting site to the Charlie-Gibbs Fracture Zone: evidence of linkage between coastal breeding seabirds and Mid-Atlantic Ridge feeding sites. Deep Sea Research Part II: Topical Studies in Oceanography, 98B, 438-444. https://doi.org/10.1016/j.dsr2.2013.04.011

Esteves, C.F., Costa, J.M., Vargas, P. et al. (2015) On the limited potential of Azorean fleshy fruits for oceanic dispersal. PLoS ONE 10, e0138882. https://doi.org/10.1371/journal.pone.0138882

Fazey, F.M.C. & Ryan, P.G. (2016) Biofouling on buoyant marine plastics: an experimental study into the effect of size on surface longevity. Environmental Pollution, 210, 354-360. https://doi.org/10.1016/j.envpol.2016.01.026

Fratantoni D.M. (2001) North Atlantic circulation during the 1990s observed with satellite-tracked drifters. Journal of Geophysical Research, 106, 22067-22093. https://doi.org/10.1029/2000JC000730

Fratantoni, D.M., Johns, W.E., Townsend T.L. et al. (2000) Low-latitude circulation and mass transport pathways in a model of the tropical Atlantic Ocean. Journal of Physical Oceanography, 30, 1944-1966. https://doi.org/10.1175/1520-0485(2000)030<1944:LLCAMT>2.0.CO;2

Friðriksson, S. & Johnsen, B. (1968) The colonization of vascular plants on Surtsey in 1967. Surtsey Research Progress Report, 4, 31-38.

Gainey, P.A. (2014) Drift seeds on Cornish strandlines. The Drifting Seed, 20, 9 – 12.

Gainey, P.A. (2020) Disseminules. In: A flora of Cornwall. (ed. Colin French), pp. 525-532. ARRC Print Ltd. Truro, Cornwall UK.

Gangopadhyay, A., Gawarkiewicz, G., Silva, E.N.S. et al. (2019) An observed regime shift in the formation of warm core rings from the Gulf Stream. Science Reports-United Kingdom, 9, 12319. https://doi.org/10.1038/s41598-019-48661-9

Goldstein, M.C., Carson, H.S. & Eriksen, M. (2014) Relationship of diversity and habitat area in North Pacific plastic-associated rafting communities. Marine Biology, 161, 1441 – 1453. https://doi.org/10.1007/s00227-014-2432-8

Gregory, M.R. (2009) Environmental implications of plastic debris in marine settings--entanglement, ingestion, smothering, hangers-on, hitch-hiking and alien invasions. Philosophical Transactions of the Royal Society B, 364, 2013–2025. https://doi.org/10.1098/rstb.2008.0265

Gunn, C.R. (1968) Stranded seeds and fruits from the southeastern shore of Florida. March/April Garden Journal, 18, 43-54.

Gunn, C.R., Andrews, J.M. & Paradine, P.J. (1984) Stranded seeds and fruits from the Yucatan Peninsula. Anales del Instituto de Biológia de la Universidad Nacional Autónoma de México. Série Botánica, 53, 21 – 60.

Gunn, C.R. & Dennis, J.V. (1999) World guide to tropical drift seeds and fruits. Malabar, Florida. Krieger Publishing Company, New York.

Guppy, H.B. (1917) Plants, seeds, and currents in the West Indies and Azores. Williams and Norgate, London.

Hamann, O. (1984) Plants introduced into Galapagos, not by man, but by El Niño? Noticias de Galapagos, 39, 15-19.

Headlam, J.L., Lyons, K., Kenny, et al. (2020). Insights on the origin and drift trajectories of Portuguese man of war (*Physalia physalis*) over the Celtic Sea shelf area. Estuarine and Coastal Shelf Science, 246, 107033. https://doi.org/10.1016/j.ecss.2020.107033

Hewitt, D.A. (2012) Southend *Nypa*, *Sepia,* fruit, and *Cocos* January 2011- April 2012. The Drifting Seed, 18, 11 - 17.

Hinata, H., Mori, K., Ohno, K., et al. (2017) An estimation of the average residence times and onshore-offshore diffusivities of beached microplastics based on the population decay of tagged meso-and macrolitter. Marine Pollution Bulletin, 122, 17 – 26. https://doi.org/10.1016/j.marpolbul.2017.05.012

Holmes, A.M., Oliver, P.G., Trewhella, et al. (2015a) Trans-Atlantic rafting of inshore Mollusca on macro-litter: American molluscs on British and Irish shores, new records. Journal of Conchology, 42, 41-49.

Holmes, A., Fenwick, D., Gainey, P. et al. (2015b) *Martesia fragilis* Verrill & Bush, 1898 in the north-east Atlantic. Overlooked and a recent new discovery. Journal of Conchology, 42(2), 183-187.

Hood, R. (2005) A 4000-mile journey to Porto Santo. The Drifting Seed, 11, 2.

Houle, A. (1998) Floating islands: a mode of long-distance dispersal for small and medium sized terrestrial vertebrates. Diversity and Distributions, 4, 201-216. https://www.jstor.org/stable/2999827

Jarzembowski, E., & Jarzembowski, B. (2014) Sea beans and ivory nuts. The Drifting Seed, 20, 17-22.

Jonsell, B.D. (2000). Flora Nordica: Chenopodiaceae to Fumariaceae. Vol. 2. Bergius Foundation, the Royal Swedish Academy of Sciences.

Kelly, D.L. (1985) Epiphytes and climbers of a Jamaican rain forest: vertical distribution, life forms and life histories. Journal of Biogeography, 1, 223-41. https://doi.org/10.2307/2844997

Kistler, L., Montenegro, Á., Smith, B.D. et al. (2014) Transoceanic drift and the domestication of African bottle gourds in the Americas. Proceedings of the National Academy of Sciences USA, 111, 2937–2941. https://doi.org/10.1073/pnas.1318678111

Kubitzki, K. & Ziburski, A. (1994) Seed dispersal in flood plain forests of Amazonia. Biotropica, 26, 30-43. https://doi.org/10.2307/2389108

Leterme, S.C. & Pingree, R.D. (2008) The Gulf Stream, rings and North Atlantic eddy structures from remote sensing (Altimeter and SeaWiFS). Journal of Marine Systems, 69, 177-190. https://doi.org/10.1016/j.jmarsys.2005.11.022

Limeburner, R., Beardsley, R.C., Soares, I.D. et al. (1995) Lagrangian flow observations of the Amazon River discharge into the North Atlantic. Journal of Geophysical Research, 100, 2401–2415. https://doi.org/10.1029/94JC03223

Liu, J., Lindstrom, A.J., Chen, Y.-S. et al. (2021) Congruence between ocean-dispersal modelling and phylogeography explains recent evolutionary history of *Cycas* species with buoyant seeds. New Phytolologist, 232, 1863 - 1875. https://doi.org/10.1111/nph.17663

Longhorn, E. (2004) Typhoons make 2004 a bumper year for sea-beans in Japan. The Drifting Seed, 10, 10.

Mazza, P.P.A., Buccianti, A. & Savorelli, A. (2019) Grasping at straws: a re-evaluation of sweepstakes colonisation of islands by mammals. Biological Reviews, 94, 1364-1380. https://doi.org/10.1111/brv.12506

Mendoza-González, G., Martínez, M.L. & Lithgow, D. (2014) Biological flora of coastal dunes and wetlands: *Canavalia rosea* (Sw.) DC. Journal of Coastal Research, 30, 697-713. https://doi.org/10.2112/JCOASTRES-D-13-00106.1

Minchin, D. (1996) Tar pellets and plastics as attachment surfaces for lepadid cirripedes in the North Atlantic Ocean. Marine Pollution Bulletin, 32, 855 - 859. https://doi.org/10.1016/S0025-326X (96)00045-8

Minchin, D. (2021) Evidence of transatlantic drift of the sea-pea *Lathyrus japonicus* subsp. *maritimus* (Fabaceae) and its recent establishment in Ireland. Cahiers de Biologie Marine, 62, 303-312.

Minchin, D. Hill, R. & Lewis, G. (2023) First record of the pan-tropical yellow water pea *Vigna luteola* (Fabaceae) seed from a NW European shore. British & Irish Botany, 5, 63-68. https://doi.org/10.33928/bib.2023.05.063

Miryeganeh, M., Takayama, K., Tateishi, Y. et al. (2014) Long-distance dispersal by sea-drifted seeds has maintained the global distribution of *Ipomoea pes-caprae* subsp. *brasiliensis* (Convolvulaceae). PLoS ONE, 9, e91836. https://doi.org/10.1371/journal.pone.0091836

Moore, C.J. (2008) Synthetic polymers in the marine environment: a rapidly increasing, long-term threat. Environmental Research, 108, 131-9. https://doi.org/10.1016/j.envres.2008.07.025

Muir, J. (1933) The beach drift of South Africa. Journal of the Botanical Society of South Africa, 10, 5-10.

Muir, J. (1937) The seed-drift of South Africa and some influences of ocean currents on the strand vegetation. Department of Agriculture and Forestry, Botanical Survey Memoir No 16. Government Printer, Pretoria.

Muñoz, J., Felicísimo, Á.M., Cabezas, F. et al. (2004). Wind as a long-distance dispersal vehicle in the Southern Hemisphere. Science, 304, 1144-1147. https://doi.10.1126/science.1095210

Murray, C.C., Maximenko, N. & Lippiatt, S. (2018) The influx of marine debris from the Great Japan Tsunami of 2011 to North American shorelines. Marine Pollution Bulletin, 132, 26 - 32. https://doi.org/10.1016/j.marpolbul.2018.01.004

Nakanishi, H. (1987) Stranded tropical seeds and fruits on the coast of the Japanese mainland. Micronesica, 20, 201-213.

Neilson, B. & Costello, M.J. (1999) The relative lengths of seashore substrata around the coastline of Ireland as determined by digital methods in a geographical information system. Estuarine, Coastal and Shelf Science, 49, 501-8. https://doi.org/10.1006/ecss.1999.050

Nelson, E.C. (1978) Tropical drift fruits and seeds on coasts in the British Isles and western Europe, 1. Irish beaches. Watsonia, 12, 103-112.

Nelson, E.C. (1986) Sea peas among tropical drift seeds. BSBI News, No 44, 16-17.

Nelson, E.C. (1990) Nickars! Or the art of growing long-distance flotsam. Moorea, 8, 2 - 13.

Nelson, E.C. (2000) Sea beans and nickar nuts: a handbook of exotic seeds and fruits stranded on beaches in north-western Europe. Botanical Society of the British Isles, London.

Nelson, E.C. (2002) Notes from Lanzarote, Canary Islands. The Drifting Seed, 8, 10.

Nelson, E.C. (2006) How far north can drift seeds be found in Eastern North America? The Drifting Seed, 12, 2 - 5.

Nichols, A.R. (1898-1901) A List of the Marine Mollusca of Ireland. Report from the Fauna and Flora Committee. Proceedings of the Royal Irish Academy, 1, 477-662. https://www.jstor.org/stable/20490561

Norton, E. (2007) The Padre Island National Seashore. The Drifting Seed, 13, 3 - 6.

Norton, E. (2008) Tropical storm Fay leaves one-day bonanza on Fort Lauderdale Beach. The Drifting Seed, 14, 3-5.

NOAA (2020) Available at https://www.nhc.noaa.gov>data (Accessed 14 November 2022)

NOAA (2021) National Hurricane Centre and Central Pacific Hurricane Centre. Available at https://www.nhc.noaa.gov/nationalsurge/ (Accessed 11 November 2022).

Ó'Foighil, D., Marshall, B.A., Hilbish, T.J. et al. (1999) Trans-Pacific range extension by rafting is inferred for the flat oyster *Ostrea chilensis*. Biological Bulletin, 196, 122 - 126.

Patterson, R. (2001) News from Bermuda. The Drifting Seed, 7, 12.

Perry, E. (2000) Beach bytes: seeds that tell stories. The Drifting Seed, 6, 11-12.

Perry, E. & Dennis, J.V. (2010) Sea-Beans from the tropics: a collector's guide to sea-beans and other tropical drift on Atlantic shores. Krieger Publishing Company, Malabar, Florida.

Póvoa, A.A., Skinner, L.F. & Vieira de Araújo, F.V. (2021) Fouling organisms in marine litter (rafting on abiogenic substrates): a global review of literature. Marine Pollution Bulletin, 166, 112189. https://doi.org/10.1016/j.marpolbul.2021.112189

POWO (2023). Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; http://www.plantsoftheworldonline.org/ (Final access 21 June 2023).

Quigley, D.T.G., Cotton, D., Pyne, A. et al. (2023) First records of laurelwood *Calophyllum* sp. (Malpighiales: Calophyllaceae) drift endocarps from Irish maritime shores and a review of NW European and western Atlantic records. Bulletin of the Irish Biogeographical Society, 46, 3-17.

Quigley, D.T.G. & Gainey, P.A. (2014) First record of an antidote vine seed *Fevillea cordifolia* L. (Cucurbitaceae) from UK and NW European waters. New Journal of Botany, 4, 176-177. https://doi.org/10.1179/2042349714Y.0000000047

Quigley, D.T.G. & Gainey, P.A. (2018) First record of a Jamaican knavel spurge *Omphalea diandra* L. (Euphorbiaceae) drift seed from NW European waters. Cahiers de Biolologie Marine, 59, 127 - 130. https://doi.10.21411/CBM.A.5C406997

Quigley, D.T.G. & MacNamara, L. (2020) A further record of a stranded Jamaican walnut endocarp (*Juglans jamaicensis* C.DC.) (Juglandaceae: Cardiocaryon) from Irish waters. Irish Naturalists' Journal, 37, 49 - 50.

Quigley, D.T.G., MacNamara, L. & Gainey, P.A. (2020a) First records of stranded nutmegs *Myristica fragrans* Houttuyn, 1774 (Magnoliales: Myristicaceae) on the Irish coast and a review of North Atlantic records. Bulletin of the Irish Biogeographical Society, 44, 178 - 188.

Quigley, D.T.G., Minchin, D. & O'Shea, J. (2020b) First record of a stranded white walnut or butternut (*Juglans cinerea* L.) (Juglandaceae: Cardiocaryon) from Irish waters. Irish Naturalists' Journal, 37, 47 - 49.

Rajabudeen, E. & Natarajan, K. (2012) Drift seeds and drift fruits from Point Calimere, Tamil Nada. Indian Journal of Tropical Biodiversity, 20, 189-192.

Rees, E.I.S. (2019) The saga of the pink bindweed (*Calystegia*) from Arthog, Merioneth (v.c.48) with additional evidence. British and Irish Botany, 1, 342-346. https://doi.org/10.33928/bib.2019.01.342

Reisser, J., Slat, B., Noble, K. et al. (2015) The vertical distribution of buoyant plastics at sea: an observational study in the North Atlantic Gyre. Biogeosciences, 12, 1249-1256. https://doi.org/10.5194/bg-12-1249-2015

Renner, S. (2004) Plant dispersal across the tropical Atlantic by wind and currents. International Journal of Plant Sciences, 165, 523 - 533. https://doi.org/10.1086/383334

Ribic, C.A., Sheavley, S.B., Rugg, D.J. et al. (2010). Trends and drivers of marine debris on the Atlantic coast of the United States 1997–2007. Marine Pollution Bulletin, 60, 1231–1242. https://doi.org/10.1016/j.marpolbul.2010.03.021

Richardson, P.L. (2005) Caribbean current and eddies as observed by surface drifters. Deep-Sea Research, Part II, 52, 429 - 463. https://doi.org/10.1016/j.dsr2.2004.11.001

Ridley, H.N. (1930) The dispersal of plants throughout the world. L. Reeve and Co., Ashford, Kent.

Rothäusler, E., Gutow, L. & Thiel, M. (2012) Floating seaweeds and their communities. In: Seaweed Biology (ed by C. Wiencke and K. Bischof), pp. 359-381. Ecological Studies, 219, Springer-Verlag Berlin Heidelberg. https://doi.org/10.1007/978-3-642-28451-9_17

Rypina, I.I., Pratt, L.J. & Lozier, M.S. (2011) Near-surface transport pathways in the North Atlantic Ocean: looking for throughput from the subtropical to the subpolar gyre. Journal of Physical Oceanography, 41, 911-925. https://doi.org/10.1175/2011JPO4498.1

Sallenger, A.H., Stockdon, H.F., Fauver, L. et al. (2006) Hurricanes 2004: an overview of their characteristics and coastal change. Estuaries and Coasts, 29, 880 - 888. https://doi.org/10.1007/BF02798647

Simpson, J.H. (1981) The shelf-sea fronts: implications of their existence and behaviour. Philosophical Transactions of the Royal Society of London, Series A, 302, 531-46. https://doi.org/10.1098/rsta.1981.0181

Sjögren, E. (1973) Vascular plants new to the Azores and to individual islands in the Archipelago. Boletim do Museu Municipal do Funchal (História Natural), 1973, 94 - 120. http://localhost:8080/xmlui/handle/100/1242

Skarpaas, O. & Stabbetorp, O.E. (2001) Diaspore ecology of *Mertensia maritima*: effects of physical treatments and their relative timing on dispersal and germination. Oikos, 95, 374-382. https://doi.org/10.1034/j.1600-0706.2001.950302.x

Sloane, H. (1698) An account of four sorts of strange beans, frequently cast on shoar on the Orkney Isles, with some conjectures about the way of their being brought thither from Jamaica, where three sorts of them grow. Philosophical Transactions, 19, 298-300.

Smith, J.M.B. (1990) Drift disseminules on Fijian beaches. New Zealand Journal of Botany, 28, 13 - 20. https://doi.org/10.1080/0028825X.1990.10412339

Smith, J.M.B. (1991) Tropical drift disseminules on southeast Australian beaches. Australian Geographical Studies, 29, 355 - 369. https://doi.org/10.1111/j.1467-8470.1991.tb00725.x

Smith, J.M.B. (1992) Patterns of disseminule dispersal by drift in the southern Coral Sea. New Zealand Journal of Botany, 30, 57 - 67. https://doi.org/10.1080/0028825X.1992.10412885

Smith, J.M.B. (1994) Patterns of disseminule dispersal by drift in the north-west Coral Sea. New Zealand Journal of Botany, 32, 453 - 461. https://doi.org/10.1080/0028825X.1994.10412932

Smith, J.M.B. (1995) Drift seed pursuits in the Coral Sea and Australia. The Drifting Seed, 1, 5-7.

Smith, J.M.B. (2006) Drift seeds and seabirds. The Drifting Seed, 12, 11-12.

Smith, J.M.B., Heatwole, H., Jones, M. et al. (1990) Drift disseminules on Cays of the Swain Reefs, Great Barrier Reef, Australia. Journal of Biogeography, 17, 5-17. https://doi.org/10.2307/2845183

Spalding, D.D. (2013) Key to the bindweeds (*Calystegia* and *Convolvulus*, Convolvulaceae) of Alabama and adjacent states. Phytoneuron, 83, 1-12.

Sullivan, G. (2004) The University of Texas at Austin Marine Science Institute (UTMSI) sea-bean collection – update. The Drifting Seed, 10, 11.

Sullivan, G. & Williams, J. (2007) UTMSI drift seed collection continues to flourish. The Drifting Seed, 13, 8 - 9.

Sullivan, G. & Williams J. (2008) A World of drift seeds. The Drifting Seed, 14, 5-10.

Sullivan, G. & Williams J. (2010) What's new on Mustang Island. The Drifting Seed, 16, 6-8.

Thiel, M. & Gutow, L. (2005) The ecology of rafting in the marine environment. The floating substrata. In: Oceanography and marine biology: an annual review 42. (ed. by R.N. Gibson, R.I.A.Atkinson and J.D.M.Gordon), pp. 181-264. Routledge, Talyor and Francis.

The Drifting Seed (1995-2015) https://www.seabean.com/newsletters/vol03-1.pdf

Van den Breme, T. and Breivik, Ø. (2017). Stokes drift. Philosophical Transactions of the Royal Society A, 376, 20170104. https://doi.org/10.1098/rsta.2017.0104

Van Duzer, C. (2004) Floating islands: a global bibliography. Cantor Press, Los Altos Hills, CA. 204pp.

Van Franeker, J.A. & Law, K.L. (2015) Seabirds, gyres and global trends in plastic pollution. Environmental Pollution, 203, 89-96. https://doi.org/10.1016/j.envpol.2015.02.034

Vatanparast. M., Takayama, K., Sousa, M.S. et al. (2011) Origin of Hawaiian endemic species of *Canavalia* (Fabaceae) from sea-dispersed species revealed by chloroplast and nuclear DNA sequences. Journal of Japanese Botany, 86, 15 - 25.

Veak, T. (2003) Exploring Darwin's correspondence: some important but lesser-known correspondents and projects. Faculty Publications and Presentations. Paper 12. http://digitalcommons.liberty.edu/lib_fac_pubs/12

Viana, D.S., Gangoso, L., Bouten, W. et al. (2016) Overseas seed dispersal by migratory birds. Proceedings of the Royal Society B, 283, 20152406. https://doi.org/10.1098/rspb.2015.2406

Vidal, N., Azvolinsky, A., Cruaud, C. et al. (2008) Origin of tropical American burrowing reptiles by transatlantic rafting. Biology Letters, 4, 115 – 118. https://doi.org/10.1098/rsbl.2007.0531

Wagner, B.F. (2002) Drift seeds of Midway Atoll National Wildlife Refuge. The Drifting Seed, 8, 7 - 8.

Walsh, W.F. & Nelson, E.C. (1987) *Lathyrus japonicus* subsp. *maritimus*. An Irish Florilegium, pp 26-28. Thames and Hudson, London.

Zies, P. (1997) Florida drift seeds. The Drifting Seed, 3, 6-7.

Zies, P. (1999) A pitch and a swing. The Drifting Seed, 5, 6.

Zies, P. (2001) Sea-bean hunting in the Amazon. The Drifting Seed, 7, 7-8.

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