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PLANT DISPERSAL ACROSS THE TROPICAL ATLANTIC BY WIND AND SEA CURRENTS

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This review brings together evidence on the monophyly and ages of angiosperm lineages ranging across the tropical Atlantic with data on the direction, strength, and speed of sea currents and wind jets across that ocean. Mainly for pragmatic reasons (data availability), the focus is on genera, which introduces a rank-based constraint into the analysis. However, trans-Atlantic disjunctions at the genus level seemed more likely to be attributable to long-distance dispersal than those involving families or species; family-level disjunctions often may date back to the breakup of Africa and South America, and species-level disjunctions often may be anthropogenic. At least 110 genera (listed in this article) contain species on both sides of the tropical Atlantic. Molecular phylogenies and age estimates from molecular clocks are available for 11 disjunct genera, tribes, and species. Inferred directions and modes of dispersal can be related parsimoniously to water currents between Africa and South America and to exceptional westerly winds blowing from northeastern Brazil to northwest Africa. Based on diaspore morphology and inferred dispersal biology in the 110 genera, trans-Atlantic dispersal by water (in both directions) appears more common than dispersal by wind or on birds. Wind dispersal appears to have occurred in the direction from South America to West Africa but rarely in the opposite direction.

Keywords: Atlantic equatorial currents, biogeography, floating islands, Gondwana breakup, transatlantic dispersal, wind dispersal.

Introduction

In an important review of tropical trans-Atlantic and trans-Pacific range disjunctions in the seed plants, Robert Thorne (1973) tabulated examples of species, genera, subfamilies, and families distributed on both sides of the tropical Atlantic. Thorne's overall goal was to assess the relative roles of Gondwana breakup compared with long-distance dispersal as causes of trans-Atlantic disjunctions. He was writing before the extent of Tertiary floristic connectivity across Beringian and North Atlantic land bridges was fully recognized (Wolfe 1975; Tiffney 1985*a*, 1985*b*; Manchester 1999) and therefore did not consider entry of lineages from the north as a third conceivable explanation for disjunct ranges between Africa and South America. That this is a real possibility is shown by phylogenetic and paleobotanical results for sublineages of legumes, Lauraceae, Malpighiaceae, and Melastomataceae (Lavin and Luckow 1993; Lavin et al. 2000; Chanderbali et al. 2001; Renner et al. 2001; Davis et al. 2002).

In the absence of information from fossils representing a taxon on both sides of the Atlantic, Thorne used taxonomic rank as a proxy for age, arguing that while it is a "truism that evolutionary rates vary greatly among different organisms," nonetheless, species formation "surely takes place much more rapidly than the evolution of genera, tribes, subfamilies, families, or even higher categories" (Thorne 1996, p. 189). Flowering plant species and genera often will be younger than 95 million years, making it likely that their presence on both sides of the Atlantic results from dispersal across that ocean. Disjunctions involving taxa at higher hierarchical levels were seen as more readily attributable from the breakup of South America and Africa. Conversely, many of the 108 species that occur in West Africa as well as in tropical America and that are mostly aquatics, maritime species, or herbaceous weeds were suspected to have reached their ranges via anthropogenic invasion.

Thorne (1973) found 111 genera that are restricted or almost restricted to South America, Africa, and Madagascar, and these form the core of his assessment that long-distance dispersal plays a small but important role in the evolution of the floras on both sides of the Atlantic. This article follows this line of thought and concentrates on genera and species. It goes beyond previous reviews of disjunct taxa (Engler 1905; Good 1964; Hepper 1965; Thorne 1972, 1973) in addressing a question that has only come within reach with the advent of DNA sequence data. Can we begin to infer the timing and direction of dispersal events in the past? With sufficient estimates (based on calibrated genetic distances, i.e., molecular clocks) we expect to see patterns in time and direction of transoceanic dispersal events because wind and water circulation systems are not randomly distributed in space and time. They should leave an evolutionary trace, provided they existed long enough to override lineage-specific differences in establishment capability (for an example, see Muñoz et al. 2004). Ideally, it should eventually become possible to use

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Table 1

Genera with Range Disjunctions between South America and Africa

Family, genus, and author	No. of total species	No. of Neotropical species	No. of African species	References and comments
Acanthaceae:				
Barleria	300 spp., mainly Africa/Asia	1? *B. oenotheroides*	200? *B. oenotheroides*	LDD dispersal from Africa to Neotropics; Balkwill and Balkwill 2002
Dicliptera Juss.	100?	84?	16	L. McDade, pers. comm., 2003
Lepidagathis Willd.	100?	1	24	L. McDade, pers. comm., 2003
Mendoncia Vell.	60	52	5	T 73
Achariaceae (ex Flacourtiaceae):				
Lindackeria C. Presl	19	13	6	T 73
Annonaceae:				
Annona L.	117	108 *A. glabra*	10 *A. glabra*, coastal West Africa	T 73; seawater dispersed; Smith 1981; Meyer 2000
Apocynaceae:				
Malouetia A. DC.	25	21	2–3, West Africa	T 73; 1 species water dispersed, several others wind dispersed; M. Endress, pers. comm., 2003
Araceae (ex Lemnaceae):				
Wolffiella Hegelm.	10	6 *W. welwitschii*	1 *W. welwitschii*	T 73; repeated LDD by seawater; Kimball et al. 2003
Arecaceae:				
Elaeis Jacq.	2	1 *E. guineensis*	1 *E. guineensis*	T 73; W. Hahn, pers. comm., 2002
Raphia P. Beauv.	21	1 *R. taedigera*	20 *R. taedigera*	T 73; LDD by seawater; Urquhart 1997
Asteraceae:				
Achyrocline (Less.) DC.	20	16	3	T 73; J. Panero, pers. comm., 2003
Aspilia Thouars (close to *Wedelia*)	60	40?	20?	T 73; J. Panero, pers. comm., 2003
Coreopsis L. (close to *Bidens*)	115	76	39	T 73; J. Panero, pers. comm., 2003
Jaumea Pers.	2?	2	1	T 73; African *Hyptis spicigera*, a tidal saltmarsh halophyte
Stenocline DC.	6	4	2?	T 73
Brassicaceae (ex Capparaceae):				
Cleome L.	150–200	100–150	50 *C. afrospina*	LDD dispersal of *C. afrospina* but not the other species; Iltis 1967
Bromeliaceae:				
Pitcairnia L'Hér.	260	260	1	T 73; LDD to West Africa by wind; Givnish et al. 2004
Burseraceae:				
Commiphora Jacq.	190	2	145 (excluding Madagascar)	LDD to South America; Weeks et al. 2004
Cactaceae:				
Rhipsalis Gaertn.	50	50 *R. baccifera*	1 *R. baccifera*	T 73 (mentioned only in text)
Chrysobalanaceae:				
Chrysobalanus L.	1–2	*C. icaco*	*C. icaco*	T 73; invasive in Pacific Islands and Hawaii, LDD by seawater
Hirtella L.	103	102	1 East Africa (!)	T 73
Clusiaceae:				
Garcinia L. (including *Rheedia* L.)	300	Needs study	Needs study	T 73; species circumscriptions and relationships very unclear; P. Sweeney, pers. comm., 2002
Symphonia L.f.	17 (16 in Madagascar)	1 *S. globulifera*	1 *S. globulifera*	T 73; LDD by seawater from Africa to Neotropics; Dick et al. 2003
Combretaceae:				
Conocarpus L.	2	2 *C. erectus*	1 *C. erectus*	T 73; mangrove species

Laguncularia C.F. Gaertn.	1	1 *L. racemosa*	1 *L. racemosa*	T 73; mangrove species
Commelinaceae:				
Buforrestia C. B. Clarke	3	1, Guianas	2	T 73; LDD very likely; R. Faden, pers. comm., 2002
Convolvulaceae:				
Calycobolus J. A. Schultes	8	5	3	T 73
Legendrea Webb & Berthel	2	1	1	T 73
Cucurbitaceae:				
Cayaponia Silva Manso	45–60	44	1	T 73
Dichapetalaceae:				
Tapura Aublet	21	17	4	T 73
Eriocaulacaceae:				
Syngonanthus Ruhland	196	195	2	T 73; LDD by wind from South America to Africa?
Euphorbiaceae:				
Amanoa Aublet	16	14	2	T 73; H.-J. Esser, pers. comm., 2002
Caperonia A. St.-Hil.	35	30	5	T 73
Maprounea Aublet	4	3	2	T 73; Esser 1999
Pogonophora Benth.	3	2	1	T 73; H.-J. Esser, pers. comm., 2002
Tetrorchidium Poepp. & Endl.	20	15	5	T 73; H.-J. Esser, pers. comm., 2002
Fabaceae:				
Andira Juss.	29	28 *A. inermis*	1 *A. inermis*	T 73; LDD by seawater; Pennington 2003
Copaifera L.	30	26	4	T 73
Desmanthus Willd.	25	25	? LDD	M. Lavin, pers. comm., 2002
Drepanocarpus G. Mey. = *Machaerium* Pers.	120	120 *M. lunatum*	1 *M. lunatum*, West Africa	LDD; Lavin et al. 2000, p. 459
Guibourtia Benn.	16	2	14	T 73
Haematoxylum L.	3	2	1	T 73
Hymenaea L.	20–25	1	1 sp., previously in *Trachylobium* Hayne	Lee and Langenheim 1975; T. Penington, pers. comm., 2003
Parkinsonia L.	19	15	4, southern and northeastern Africa	T 73
Pentaclethra Benth.	2	1	1	T 73
Pomaria Cav.	15	12, New World	3, southern Africa	Simpson 1998, 1999; B. Simpson, pers. comm.
Gelsemiaceae (ex Loganiaceae):				
Mostuea Didrichsen	8	1	7	T 73
Gentianaceae:				
Neurotheca Benth.	3	1 *N. loeselioides*	1 *N. loeselioides*	T 73; age unknown; Struwe et al. 2002, p. 220
Schultesia Mart.	15	14 *S. stenophylla*	1 West Africa *S. stenophylla*	T 73; LDD likely; Struwe et al. 2002, p. 220
Voyria Aublet	19	1	18	T 73; Albert and Struwe 1997; Struwe et al. 2002, p. 266
Hernandiaceae:				
Gyrocarpus Jacq.	5	3, but *G. americanus* polyphyletic	3, but *G. americanus* polyphyletic	Repeated LDD by seawater; S. Renner and B. Zhang, unpub. MS
Hernandia L.	20 (also Polynesia, Australia)	9	2	LDD from Neotropics to Bioko by seawater; Kubitzki 1969
Humiriaceae:				
Sacoglottis Mart.	8	7	1	T 73; LDD of ancestor of African *S. gabonensis* by seawater
Lamiaceae:				
Hyptis Jacq.	300?	? *H. spicigera*	2 *H. spicigera*	T 73
Lauraceae:				
Ocotea Aublet	330	300	7	T 73; Chanderbali et al. 2001

Table 1

(*Continued*)

Family, genus, and author	No. of total species	No. of Neotropical species	No. of African species	References and comments
Lentibulariaceae:				
Utricularia L.	180 worldwide	Needs study, *U. juncea*	Needs study, *U. juncea*	Taylor 1989; Dörrstock et al. 1996
Malpighiaceae:				
Heteropterys Kunth	120	119 *H. leona*	1, coastal West Africa *H. leona*	T 73; probably introduced by man; Anderson 1990, 2001
Stigmaphyllon A. Juss.	90	89	1, West Africa	T 73; *S. bannisterioides* probably introduced by man; Anderson 1990, 1997
Malvaceae:				
Carpodiptera Griseb.	6	4	2	T 73
Ceiba Mill.	1	1 *C. pentandra*	1 *C. pentandra*	LDD from Neotropics to Africa; C. Dick, pers. comm., 2003
Christiana DC.	4–5	2 *C. africana*	1 *C. africana*	T 73
Marantaceae:				
Thalia L.	7	7 *T. geniculata*	1 *T. geniculata*	T 73; LDD by seawater
Mayacaceae:				
Mayaca Aublet	4	3	1	T 73; invasive aquatics
Meliaceae:				
Carapa Aublet	2–7	? *C. guianensis*	? *C. guianensis*	T 73; LDD from Africa to Neotropics, drifting seeds; Gunn 1968
Guarea L.	40	35	5	T 73
Moraceae:				
Dorstenia L.	105	46	48	Berg 2001; C. Berg, pers. comm., 2003
Maclura (including *Chlorophora* Gaudich.)	11	2	1, East Africa, Madagascar	T 73; C. Berg, pers. comm., 2003
Trophis P. Browne	9	5	2, Madagascar, Reunion, Comores	Berg 2001; C. Berg, pers. comm., 2003
Ochnaceae:				
Sauvagesia L.	32	30 *S. erecta*	2 *S. erecta*	T 73; LDD likely; V. Bittrich, pers. comm., 2002
Olacaceae:				
Aptandra Miers	4	3	1	T 73; D. Nickrent, pers. comm., 2002
Heisteria Jacq.	40	37	3	T 73
Ptychopetalum Benth.	4	2	2	T 73
Menodora Bonpl.	25	22	3, South Africa	T 73
Orchidaceae:				
Diceratostele Summerh./ *Palmorchis* Barb. Rodr.	30?	30?	1 *D. gabonensis*, West Africa	Dressler 1981
Pteroglossaspis Rchb.f.	5	4, Cuba, Argentina	1, East Africa and Madagascar	T 73; LDD dispersal by wind at least for *P. ruwenzoriensis*
Pedaliaceae:				
Rogeria Delile	6	1	5	T 73
Poaceae:				
Ctenium Panz.	2	10	10	T 73; L. Clark, pers. comm., 2002
Echinolaena Desv.	6	5	1	T 73
Eriochrysis P. Beauv.	7–8	3–4	4	T 73
Euclasta Franch.	3	2–3	1, tropical Africa	T 73
Loudetia Steud.	20	1	19	T 73; L. Clark, pers. comm., 2002
Olyra L.	22	22 *O. latifolia*	1 *O. latifolia*	T 73; *O. latifolia* introduced by man?

Orthoclada P. Beauv.	2	1	1, southeast Africa	T 73; L. Clark, pers. comm., 2002
Paratheria Griseb.	2	2	1?	T 73
Sorghastrum Nash	12	7	5	T 73
Trachypogon Nees	3	2	1	T 73
Trichoneura Andersson	9	3, U.S.A., Peru, Galapagos	6	T 73
Willkommia Hack.	5	1, U.S.A.; 1 Argentina	3	T 73
Polygonaceae:				
Symmeria Benth.	1	1 *S. paniculata*	1 *S. paniculata*, West Africa	T 73
Pontederiaceae:				
Eichhornia A. Rich.	5	5	1	T 73; *Eichhornia crassipes* introduced by man?
Heteranthera Ruiz & Pav.	10	7	3	T 73
Rapateaceae:				
Maschalocephalus Gilg & K. Schum.	1	1 *M. phalus dinklagei*	1 *M. dinklagei*, West Africa	Givnish et al. 2000, 2004
Rhizophoraceae:				
Cassipourea subgen. *Cassipourea*	62	9	Unclear species numbers	LDD inferred from genetic distances; A. Schwarzback, pers. comm., 2002
Rhizophora	6	2 *R. mangle*	1 *R. mangle*, West Africa	LDD inferred from genetic distances; A. Schwarzback, pers. comm., 2002
Rubiaceae:				
Bertiera Aublet	28	2 *B. guianensis* in east Brazil; *B. bracteosa* in Ecuador!	16	T 73; Andreasen and Bremer 2000
Mitracarpus Schult. & Schult. f.	30	30	1 West Africa and Madagascar	T 73; *M. scaber* introduced by man? Bremer and Manen 2000
Pentodon Hochst.	2–3	1 *P. pentandrus*	1 *P. pentandrus*	T 73; apparently a global weed; Bremer and Manen 2000
Sabicea Aublet	130	40	82	T 73; Bremer and Thulin 1998
Rutaceae:				
Thamnosma Torr. & Frém.	6–10	4, also North America	2, also Socotra	T 73
Sapindaceae:				
Paullinia L.	180–200	180–200	1	T 73
Sapotaceae:				
Chrysophyllum including *Gambeya* Pierre	25	11	14	T 73; Pennington 1990
Solanaceae:				
Lycium L.	100	84?	16 South Africa	LDD possible; L. Bohs, pers. comm., 2002
Schwenkia L.	10	10 *S. americana*	1 *S. americana*	T 73; *S. americana* introduced by man?
Turneraceae:				
Turnera sect. *Piriqueta*	19	18	1	T 73
Ulmaceae:				
Celtis L. (subg. *Mertensia*)	Needs study	Needs study	Needs study	Berg and Dahlberg 2001; C. Berg, pers. comm., 2003
Urticaceae:				
Phenax Wedd.	12	12	1	T 73; introduced by man and naturalized in Africa and Madagascar?
Verbenaceae:				
Lippia L.	200	185	15	T 73
Zingiberaceae:				
Renealmia L.f.	75	50	25	T 73; Maas 1977

Sources. Based on Thorne (1973; abbreviated “T 73”) and additional sources as indicated. Family circumscriptions follow APG II (2003).

Note. Species numbers are usually only rough estimates because of a dearth of monographic work. Epithets are provided for species occurring on both sides of the Atlantic, sometimes possibly due to anthropogenic introductions. LDD = long-distance dispersal. “Excluded” refers to transfers of species published after the compilation of Thorne (1973).

models of ocean and wind circulation patterns to test inferred directions and times of dispersal events.

Given that there is only a loose connection between dispersal and permanent establishment of a lineage, it is clear that numerous taxa will need to be compared before one expects patterns to emerge. To augment the limited data from flowering plants, the discussion below therefore includes three particularly well-studied trans-Atlantic animal disjunctions to illustrate the kinds of data that need to be evaluated and as a reminder that plants are not the only organisms that crossed the Atlantic; so did monkeys, rodents, and lizards.

Material and Methods

Lineages with tropical trans-Atlantic distributions were compiled from the literature, starting with Thorne's (1973) list of 111 genera of seed plants restricted to tropical and temperate America and Africa (including Madagascar and African Islands). The focus on genera centered in South America and Africa (leaving out pantropical genera and taxa at other hierarchical levels) was mainly pragmatic: (1) There is no doubt that plant diaspores are constantly exchanged between Africa, Madagascar, India, and the Malesian region via migratory bird flyways, sea currents, and wind, and the list of taxa disjunct between Africa/Madagascar/Asia accordingly comprises several hundred genera (Thorne 1973). A compilation of such relatively uncontroversial dispersal events would have led far beyond my goal of trying to link inferred dispersal directions and times with surface sea currents and winds in a clearly circumscribed system. (2) The initial focus on genera, while introducing a rank-based constraint into the analysis, is justified by the probability of disjunctions at that level often having explanations postdating the breakup of Africa and South America, i.e., dispersal by water, wind, or birds. Disjunctions involving families will often be attributable to the breakup of Gondwana and those involving species to anthropogenic dispersal (e.g., in pantropical weeds). Wherever available, studies on trans-Atlantic clades at higher or lower hierarchical levels were included (e.g., Melastomeae; *Symphonia globulifera*), but their number is very small.

Thorne's list of genera was updated via a literature search and input from specialists (named in table 1), who reviewed entries for individual families and added information on ongoing molecular systematic work. Paleoclimatic and oceanographic data came mostly from recent literature. Of key importance was evaluation of the evidence for monophyly of the disjunct genera. Where molecular data suggest that a trans-Atlantic disjunct genus is polyphyletic and that African and South American species are more closely related to species on the same continent than on the opposite continent, this "pushes" disjunction events in the respective lineage further back in time, perhaps to the breakup of West Gondwana. Where molecular data reveal that African or Neotropical species are nested within genera occurring on the opposite continent, this increases the number of lineages for which trans-Atlantic diaspore dispersal may need to be invoked. To detect such nesting (i.e., paraphyly), systematists need to sample widely, and on both sides of the Atlantic, which may present more than logistic problems because many of us tend to be continent specialists and may not have the overview necessary to know which taxa from another continent ought to be included in a study. This difficulty, together with the problems of obtaining material from several continents (with various collecting restrictions), may be at the root of why so little is known about tropical range extensions, be they due to natural or anthropogenic long-distance dispersal.

Results

Some 110 angiosperm genera in 53 families (table 1) contain species on both sides of the tropical Atlantic. Even though these numbers are almost identical to Thorne's (1973), 16 newly recognized disjunct genera were added and 14 others were dropped because they are no longer considered monophyletic (appendix). The disjunction in the range of one other genus, *Genlisea*, is no longer seen as the result of long-distance dispersal, but instead is explained by entry from the boreotropics (Jobson et al. 2003).

At present, molecular phylogenetic results (topologies and initial molecular clock datings) are available for 11 trans-Atlantic disjunct lineages (table 2), namely, *Cassipourea*, *Ceiba pentandra*, *Commiphora*, *Elaeis oleifera*, *Maschalocephalus dinklagei*, *Pitcairnia feliciana*, *Raphia*, *Rhizophora*, *Symphonia globulifera*, *Wolffiella welwitschii*, and the ancestor of a group of genera in the Melastomeae (references, table 2).

A striking pattern evident from table 2 is that the four dispersals from South America to Africa are all inferred to have involved wind, whereas dispersal from Africa to South America is inferred to have involved sea currents. At least the latter probably is a sampling artifact. Inspection of table 1, which includes all 110 trans-Atlantic disjunct genera, indicates several cases of likely dispersal by water from South America to Africa, namely, *Andira*, *Drepanocarpus*, *Hernandia*, *Hymenaea*, *Sacoglottis*, and *Thalia* (possibly also *Cayaponia*).

There are two instances of previously unrecognized paraphyletic lineages added to Thorne's (1973) list: the Neotropical Fabaceae *Hymenaea* includes a species from Africa, *Trachylobium verrucosum* (Lee and Langenheim 1975), and Neotropical *Celtis* section *Mertensia* probably includes some or all of African *Celtis* (C. C. Berg, personal communication, 2003).

Discussion

Current understanding of the timing and direction of long-distance dispersal across the Atlantic is still very limited, and complementary studies that would focus on anthropogenic introductions are in their infancy. Studies of possible anthropogenic dispersal in tropical species, perhaps with slave ships or modern transport, could begin with the 108 species of angiosperms spanning the Atlantic (Thorne 1973). Such phylogeographic work, of course, would require population-level sampling. However, with one exception, studies on tropical trans-Atlantic clades so far have sampled single accessions per species on the African and South American continents. The exception is a phylogeographic study of a trans-Atlantic disjunct tree species that includes multiple accessions from both sides of the Atlantic (Dick et al. 2003).

Table 2

Angiosperm Dispersal across the Tropical Atlantic

Taxon	South America to Africa	Africa to South America	Inferred means of dispersal	Reference
Arecaceae, *Elaeis oleifera*	. . .	Recent	Water	W. Hahn, pers. comm., 2002
Arecaceae, *Raphia taedigera*	. . .	Recent	Water	Urquhart 1997; W. Baker, pers. comm., 2003
Bromeliaceae, *Pitcairnia feliciana*	8 Ma	. . .	Wind	Givnish et al. 2004
Burseraceae, *Commiphora*	. . .	Recent	?	Weeks et al. 2004
Clusiaceae, *Symphonia globulifera*	. . .	3 events, all recent	Water	Dick et al. 2003
Lemnaceae, *Wolffiella welwitschii*	. . .	9.8 Ma, 2 events	Water	Kimball et al. 2003
Malvaceae, *Ceiba pentandra*	Recent	. . .	Wind or anthropogenic	C. Dick, pers. comm., 2003
Melastomataceae, Melastomeae	11 Ma	. . .	Wind	Renner and Meyer 2001
Rapateaceae, *Maschalocephalus dinklagei*	6 Ma	. . .	Wind	Givnish et al. 2000, 2004
Rhizophoraceae, *Cassipourea*	. . .	Recent	Water	A. Schwarzbach, pers. comm., 2002
Rhizophoraceae, *Rhizophora*	. . .	Recent	Water	A. Schwarzbach, pers. comm., 2002
Platyrrhine monkeys	. . .	33–35 Ma	Water	Lavocat 1980; Houle 1999; Nei et al. 2001
Caviomorph rodents	. . .	85 Ma or 43 Ma	Water, but assumed source controversial	(43 Ma) Lacovat 1974; (43 Ma) Huchon and Douzery 2001; (85 Ma) Mouchaty et al. 2001
Mabuya lizards	. . .	9 Ma	Water	Carranza and Arnold 2003

Note. "Recent" refers to geological times with ± present-day distances between Africa and South America and before the advent of humans. Standard errors on the molecular clock–based estimates appear in the cited sources.

From the current data, it appears that transport by surface sea currents has been responsible for successful dispersals in either direction, while winds seem to have played more of a role in diaspore transport from South America to Africa (tables 1, 2). This surprising result (if valid) raises the question whether oceanographic and climatic data indicate different predominant directions of water versus wind currents that would explain these apparent differences in their relative roles in conveying biological material from east to west versus west to east.

Ocean Currents

The tropical Atlantic's major currents vary in strength with the seasons and comprise a westward-flowing North Equatorial Current (NEC), an eastward-flowing North Equatorial Counter Current (NECC), and a westward-flowing South Equatorial Current (SEC) (fig. 1). Although local surface circulation in the east tropical Atlantic is not yet adequately known (Fratantoni 2001), satellite-tracked surface drifters have shown that water movement is very quick in the equatorial region, with typical speeds approaching 1 m s^{-1}. (Ocean near-surface drifter data recorded during the 10-yr world ocean circulation experiment are available from the Atlantic Oceanographic and Meteorological Laboratory/NOAA.)

The high drift speeds in some stretches of the Atlantic agree with information from nautical maps (Houle 1999) that reflect accumulated knowledge from tens of thousands of trans-Atlantic crossings by a range of vessels. The two belts in the tropical Atlantic where surface currents and winds are simultaneously favorable for east to west crossing lie between the Congo delta and Maranhão in Brazil (a band between ca. 5°N and 10°S; fig. 1) and just north of the Senegal River delta and northern Brazil and the Guianas (between 10° and 30°N; Houle 1999). Both of these surface currents start from river deltas in Africa. The only surface current running in the opposite direction is the NECC, which, however, originates well off the South American coast (fig. 1) and therefore may not be optimally suited for transporting plant parts from northern South America to West Africa.

It is unlikely that the main direction of these currents has changed since the breakup of West Gondwana (Parrish 1993; K. Nisancioglu, personal communication, 2003). Indeed, Parrish (1993, p. 17) suggests that rafting of organisms between South America and Africa during the Tertiary is "likely to have been predominantly east to west rather than the reverse," in agreement with the data in table 2. Surface current systems arise as a result of horizontal pressure gradients induced by the wind and the Coriolis force. In the central Atlantic, they may have been slightly different during the Eocene warm climates; however, there is no good proxy for wind patterns from Tertiary periods, and present wind fields are therefore used in paleo-ocean models (K. Nisancioglu, personal communication, 2002). During the Miocene, at the time of the shoaling of the Central American seaway, the physical mechanism driving the currents (i.e., the winds) would have been the same as today, and the only part of the surface circulation that is assumed to have been different is that in the immediate vicinity of the closing isthmus. Almost certainly, the two current systems in the northern South Atlantic (the NEC and NECC) would have been the same before and after the closing of the isthmus (K. Nisancioglu, personal communication, 2003).

The extent to which fluctuations in the depth of the Atlantic during the Tertiary narrowed the distance between continents and provided stepping stone islands is controversial. Shortest linear distances between Africa and South America have increased from ca. 1000 km at 50 Ma to 1900 km at

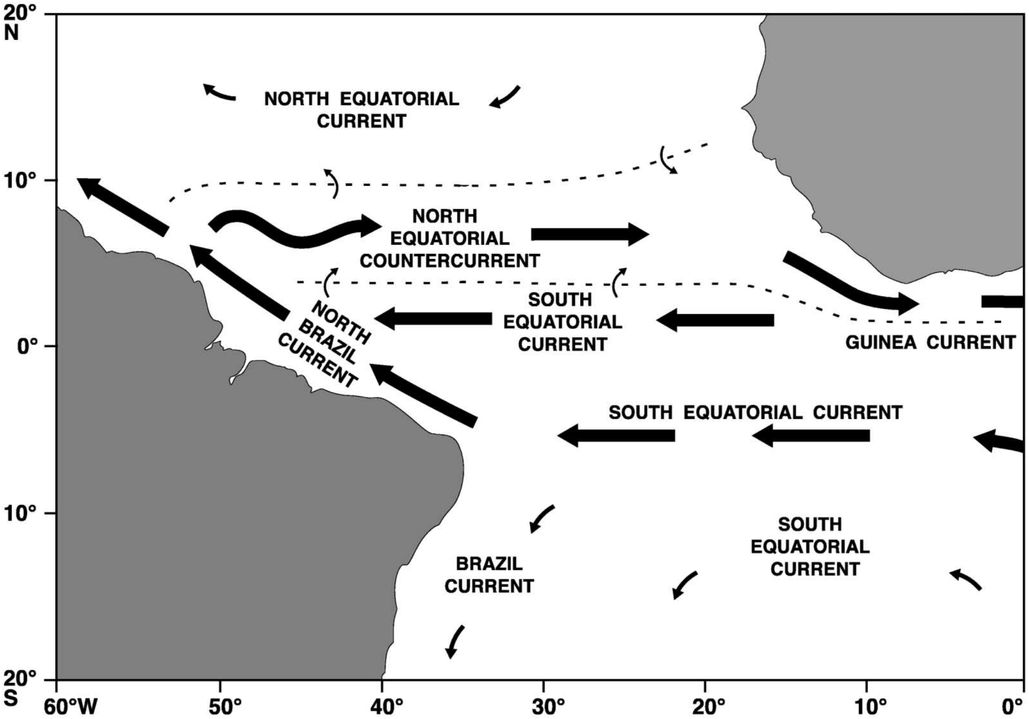

Fig. 1 The major tropical Atlantic surface currents (after Fratantoni et al. 2000)

30 Ma, while "sailing distances," that is, distances covered by surface sea currents and winds, always were ca. 100 km longer (Houle 1998 tabulates both kinds of distances for various times in the past). Ocean drilling and sonar studies in the southern South Atlantic have shown that the Rio Grande rise (southeast of the coast of Brazil at about the height of Rio de Janeiro) and the western end of the Walvis Ridge (southwest of the coast of Africa at about the height of Cape Town) may have been above water as late as the Oligocene (Parrish 1993; Morley 2000, fig. 12.2), which would have greatly narrowed the distance between the continental coasts. Ocean-floor drilling data are sparser for the northern South Atlantic (Parrish 1993), but the Vema Transverse Ridge, which offsets the Mid-Atlantic Ridge by 320 km and today is 600 m below sea level, has been found to be capped by carbonate platforms (reef limestone) that formed at ca. 3–4 Ma (Kastens et al. 1998). Of course, the Mid-Atlantic Ridge itself rises above sea level in several island chains, including St. Paul's Rocks almost exactly on the equator. The species-poor animal and plant floras of these islands may not be indicative of the frequency of biological transport across other regions of the Atlantic, as suggested by inspection of surface drifter trajectories from the World Ocean circulation experiment (see maps in Fratantoni 2001).

Several dispersal events involving vertebrates are relevant to the above discussion of plant dispersal across the Atlantic. They involve the ancestors of Neotropical caviomorph rodents, platyrrhine monkeys, and lizards. The earliest Caviomorpha fossils in South America are 34–32 m.yr. old, and the earliest Platyrrhini fossils are 26 m.yr. old. Both lineages have close relatives in Africa (Mouchaty et al. 2001, but see below; Nei et al. 2001) and neither has fossils in North America, Antarctica, or Australia that would indicate alternative source areas (Houle 1999). Recent reviews (Houle 1998, 1999) of oceanic rafting by small vertebrates (focusing on the tropical Atlantic) tabulate the transport speed of variously shaped objects. Houle's calculations of the times needed for objects to travel from Africa to Brazil or Venezuela are based on nautical charts and incorporate either just the velocity of the surface current or current speed plus wind velocity, as well as a slightly narrower tropical Atlantic at 50, 40, and 30 Ma. Floating islands relevant to the postulated migrations of monkeys and rodents probably carried shrubs or trees and therefore were helped along by the trade winds. Without some shade-providing vegetation, it is unlikely that any vertebrates would have survived over a week of sun exposure and dehydration. Records of floating islands, one measuring 60 m × 23 m, with trees as high as 15 m, are reviewed in Houle (1998), although there is no record of such an island far off the coasts of Africa or Brazil. Even so, migration on a floating island appears to be the best explanation for the Oligocene/Miocene arrival of platyrrhines in South America.

For Caviomorpha, exact relationships of South American, African, and Asian lineages are still unclear (cf. Mouchaty et al. 2001 and Huchon and Douzery 2001), but rafting across some water barrier is inferred by all studies. The same holds for several tropical American lizard groups that, according to DNA evidence, arrived by trans-Atlantic dispersal from Africa during the last 10 m.yr., once reaching the American mainland and once the oceanic island of Fernando de Noronha, two journeys each of at least 3000 km (Carranza and Arnold 2003 and references therein).

Wind Currents

It is more difficult to account for dispersal events inferred to have been due to winds blowing from South America to Africa (table 2). So far, four such instances involving Bromeliaceae, Melastomataceae, Rapateaceae, and possibly Malvaceae are suggested by molecular topologies and dating. Westerly surface winds over the central Atlantic (10°S–5°N, 40°W–0°E) exist but are subject to significant year-to-year changes. They result from the pressure trough over the Sahara, which in some years turns both northern and southern trade wind systems toward the continent, resulting in the West African monsoon. Westerly wind jets may exceed near-surface speeds of 10 m s^{-1} and even 15 m s^{-1} and may extend across the entire Atlantic basin, although they very rarely, for example, on August 17, 1999, occur over the South American coast (Grodsky et al. 2003; S. A. Grodsky, personal communication). These wind jets appear in May and persist through September, with their latitudinal position following the meridional migration of the Intertropical Convergence Zone (ITCZ). Years with strong near-surface westerly winds tend to correlate with tropical storms and hurricanes over the western Atlantic (Grodsky et al. 2003) and with African rainfall patterns (Jury et al. 2002). Storms also occasionally blow in the other direction (from Africa to South America), and dust is regularly swept out over the Atlantic Ocean from the Sahara Desert, sometimes blowing all the way to North and South America (http://earthobservatory.nasa.gov/). Even desert locusts, *Schistocerca gregaria*, are occasionally (e.g., in 1950 and 1988) transported alive from Africa to Surinam, Guyana, or the West Indies (Tipping 1995).

Transport on Birds

Dispersal of seeds across the tropical Atlantic by aquatic birds, for example, ducks, is an oft-mentioned possibility, most explicitly perhaps by Iltis (1967), who adduces the ranges of trans-Atlantic disjunct duck sister species as an argument in favor of past trans-Atlantic seed dispersal by these ducks. However, there are no bird migratory routes across the Atlantic, and the cattle egret, *Bubulcus ibis*, which apparently flew over the Atlantic sometime around 1880, established in Brazil, and from there spread to North America, remains the only documented case of a trans-Atlantic colonization event by a bird (Terres 1991). The cattle egret feeds on insects (Terres 1991), and I have located no records of seeds it may transport. Marine birds rarely if ever eat seeds or fruits, and frugivorous land birds usually vacate their guts frequently (every few minutes; Snow and Snow 1988; White and Stiles 1990). A fruit-eating bird blown offshore by a storm is very unlikely to retain gut content across the Atlantic. This leaves the possibilities of seeds sticking to the feet or feathers of marine or shore birds, which, however, requires that a plant species occurs in the habitats frequented by these birds and has the necessary morphological adaptations (Carlquist 1981). That land birds (and seeds) nevertheless have occasionally reached the Mid-Atlantic islands is shown by endemic bird species, such as on Tristan da Cunha, which has five land bird species, a rail, a moorhen, a thrush, and two buntings (Sibley and Monroe 1990).

Conclusion

Tangled plant parts (“floating islands”) are constantly carried out into the tropical Atlantic from the deltas of the Congo, Senegal, and Amazon rivers, and some enter the conveyer belt–like currents that transport debris (including plastic trash; Barnes 2002) in either direction across the Atlantic. Because of their speed, equatorial currents can transport larger floating objects with wind-exposed surfaces across the Atlantic in less than 2 weeks, and transport was probably faster across the narrower Atlantic of the Early Tertiary. Successful dispersal of diaspores by wind or stuck on birds appears to be less common. It is also possible that minute seeds, such as those of Melastomataceae, which are known to be abundant in tropical soils (Dalling et al. 1998), crossed the Atlantic in soil stuck to drifting vegetation rather than being carried by exceptional westerly winds or hurricanes. Indeed, if monkeys and rodents arrived on a uniquely successful floating island, that same island would have brought lots of seeds, insects, and lower organisms.

Judging from the slow increase in our understanding of timing and direction of successful dispersal events across the Atlantic over the 30 years since Robert Thorne’s review of the topic in 1973, an overly optimistic outlook is not warranted. However, empirical and model-derived oceanographic and climatic data now make it easier for botanists than it was in the 1970s to envision rapid Atlantic crossings along specific sea and wind currents, sometimes followed by successful establishment of a lineage.

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Appendix

Genera previously (e.g., Thorne 1973) seen as occurring on both sides of the Atlantic but now seen as polyphyletic include the following: (1) *Schaueria* Nees, sole African species excluded (L. McDade, personal communication); (2) *Thyrsodium* Benth., sole African species excluded (A. Miller, personal communication); (3) *Chrysocoma* L. and (4) *Tarchonanthus* L., in both cases, Neotropical species excluded (J. Panero, personal communication); (5) *Acioa* Aublet, African species transferred into *Dactyladenia* (genera may be sister groups; C. Morton, personal communication); (6) *Vismia* Vand., African species transferred to *Harungana* (genera may be sister groups; M. Gustafsson, personal communication); (7) *Paepalanthus* Mart., African species excluded;

(8) *Savia* Willd., African species excluded; (9) *Conceveiba* Aublet, both African species transferred to *Aubletiana* (Murillo 2000); (9) *Newtonia* Baill., Neotropical species excluded; (10) *Swartzia* Schreb., African species transferred into *Bobgunnia* J. H. Kirk. & Wiersema (Ireland et al. 2000); (11) *Hoffmannseggia*, the three African species transferred to *Pomaria* (Simpson and Lewis 2003; Simpson et al. 2003); (12) *Landolphia* P. Beauv., the two Neotropical species now recognized as a separate genus *Pacouria* (M. Fallen, personal communication); (13) *Sphaeralcea* A. St.-Hil., African species excluded (C. Bayer, personal communication); (14) *Trymatococcus* Poepp. & Endl., African species transferred into *Dorstenia* (C. C. Berg, personal communication).

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