Plant dispersal and the origin of Pacific island floras

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Introduction and historical review

Evidence for long distance dispersal to oceanic islands is enormous, as the review below will show. However, long distance dispersal has not been uniformly believed as accounting for floras of what are generally regarded as oceanic islands, and some biologists have imagined such geological phenomena as former land bridges or now-vanished continents to explain the biota of these islands. The reasons for such disbelief in the efficacy of long distance dispersal are various, but pivot on the rarity of successful establishments on oceanic islands, and therefore the necessity of postulating a past event that was not observed by scientists. This circumstance is by no means unique in science, since geological and astronomical events are not subject to direct experimental verification either. The endemic nature of species on oceanic islands is indirect evidence of rarity of successful establishments, a necessary correlation because frequent reintroduction of a species prevents development of an endemic derivative. However, those who are skeptical about long distance dispersal would, ironically, like to see those extremely rare actual events of establishment that result in production of endemic species in order to believe in the process.

Frequent events of dispersal are not contested: the flotation of seeds that arrive in huge quantitites on beaches and which therefore populate Pacific atolls (which are, in effect, mid-ocean beaches) with species does not seem in contention. For those skeptical about long distance dispersal, credulity falters not with regard to atoll floras, but where the inland floras of high islands are concerned.

Curiously, long distance dispersal to continental islands ought to inspire disbelief in those who are skeptical about dispersal to volcanic high islands, but it seems not have done so. Once a continental island separates from a larger land mass, dispersal to the island is by definition dispersal across oceanic distance, distance that generally increases over time by virtue of tectonic plate movements. Can anyone doubt that such elements as *Helichrysum* (Asteraceae), or genera of Myrtaceae (*Melaleuca*, *Metrosideros*, *Xanthostemon*) and Epacridaceae (*Dracophyllum*, *Styphelia*) on New Caledonia are relatively recent arrivals on New Caledonia? Similarly, can anyone question that any of the Asteraceae on New Zealand are recent arrivals? Asteraceae are a family of recent (upper Oligocene) origin, and the primitive stocks are mutisioids, broadly construed (Jensen *et al.*, 1991), whereas New Zealand Asteraceae do not qualify as primitive within the family. The fact that New Caledonia and New Zealand are old continental islands permits those skeptical about long distance dispersal to believe that any or all phylads might have arrived on these islands prior to separation of larger land masses.

isms known to be likely of recent origin (see McDowall, 1976). Nevertheless, I am not aware of any attempt to list the floristic contents of New Caledonia or New Zealand according to relict and long distance dispersal categories – a task that eventually should be done. The existence of clear examples of recent arrivals, such as *Helichrysum* on New Caledonia, or any of the Asteraceae on New Zealand, is sufficient to establish the existence of the phenomenon.

Interestingly, long distance dispersal has had strong advocates from the earliest days in understanding of island floras. Validation of long distance dispersal was essential to the promulgation of Darwin's (1859) theory of evolution, because if the same species occurs on two widely separated oceanic islands, or an oceanic island and a mainland area, one must hypothesize dispersal to account for the distribution or else one must hypothesize independent evolution of the same species on two different occasions independantly – the latter quite unlikely in Darwin's view.

Darwin (1859) cites some good examples of potential external seed dispersal on birds: 'Mr. Swaysland, of Brighton, who during the last forty years has paid close attention to our migrating birds, informs me that he has often shot wagtails, wheat-ears, and whinchats, on their first arrival on our shores, before they had alighted; and he has several times noticed little cakes of earth adhered to their feet....Prof. Newton has sent me the leg of a red-legged partridge (*Cacabis rufa*) which had been wounded and could not fly, with a ball of hard earth adhering to it, and weighing six and a half ounces. The earth had been kept for three years, but when broken, watered and placed under a bell glass, no less than 82 plants sprung from it..' Hooker's influential 1866 lecture on insular floras (reprinted, with comments, by Williamson, 1984) also underlines the role of long distance dispersal, even if Hooker did not have the data that would have enabled him to understand why the Azores flora lacks American affinities. The Azores flora is better explained by Wallace (1880) in 'Island Life,' a book in which an entire chapter is devoted to dispersal, mostly what we would now call long distance dispersal.

If one could fault Darwin, Hooker, and Wallace in any respect, it would be in their overemphasis on seawater flotation as a potential means of populating oceanic islands with plants. This bias is entirely understandable, be-easier than with other means of dispersal.

Other strong advocates for the existence of long distance dispersal in past decades include Skottsberg (1925, 1928, 1940), who dealt chiefly with the Juan Fernandez and the Hawaiian Islands; and Ridley (1930), who surveyed dispersal as a whole. Fosberg (1948) clearly underlined the role of long distance dispersal in his survey of the Hawaiian flora. Beginning with such varied and auspicious advocacy of long distance dispersal as capable of accounting for the floras of oceanic islands, one is surprised that belief in the efficacy of the process has faltered at all.

Among skeptics, one can cite, in relatively recent decades, van Steenis (1962) and Love and Love (1967). Van Steenis may have been influenced by working primarily with Malesian areas with essentially continental floras. Ironically, van Steenis believed that mountains such as Kinabalu (Sabah, Borneo) received its immigrants across continuous land, whereas even if continuous land existed between Kinabalu and its various source areas, long stretches of land unsuitable for alpine genera such as *Gentiana* and *Ranunculus* must always have separated alpine Kinabalu from alpine areas of other mountains – gaps that are explainable only by long distance dispersal, because unbroken interconnecting land at alpine elevations is so unlikely. Love and Love (1967) thought that the high-latitude Arctic floras were once continuous, and have differentiated after separations of the continents and islands by tectonic drift. Ironically, these workers were best acquainted with the flora of their native land, Iceland, a definitive and recent oceanic island formed on the Mid-Atlantic Ridge.

In fact, most biologists, especially those who have dealt with remote volcanic islands such as the Hawaiian chain, readily credit the efficacy of long distance dispersal as a means for populating oceanic islands. The only challenge of recent years has come from proponents of a strict kind of 'vicariance biogeography,' notably Ball (1975), Nelson (1973, 1974), Platnick (1976) and Rosen (1975). The attempt of these workers to develop 'generalized tracks' by superimposing phylogeny of groups onto geographic patterns and developing schemes for migration of entire biotas in accordance with these generalized tracks. The stinging critique of McDowall (1976) of the methods employed by these authors could suffice to neutralize their antidispersalist

dogma, but we need to understand why adherents of 'vicariance biogeography' dismissed the possibilities of long distance dispersal so summarily. First, none of the advocates of vicariance biogeography worked closely with floras or faunas of Pacific oceanic islands: Rosen worked with primary division freshwater fish, which have very conservative biogeographic patterns. More significantly, vicariance biogeography was an attempt to find a way to approach statistical significance in interpretation of biogeographic patterns, parallelling the developments in the 1970's in application of statistical methods to ecology and evolution. However, as McDowall (1976) notes, vicariance biogeographic methods fall short of statistical significance – no quantitative criteria for definition of tracks are given. If we are dealing with patterns based upon tectonic plate movement, 'generalized tracks' (but ones not as precisely definable as the geological events, if known in detail, to which they are related) can be claimed, but any distribution pattern resultant from long distance dispersal would add a 'noise level' to such patterns. Floras such as the Hawaiian, in which origins are entirely from long distance dispersal and which can be traced to source areas in all directions would be, in this regard, ALL noise level, with no 'generalized tracks' evident. Long distance dispersal, therefore, posed a threat to vicariance biogeography methods, and had to be rejected by adherents of that methodology except as a minor influence at best. No advocate of vicariance biogeography has seriously attempted to explain the Hawaiian flora or fauna. Some have inferred the existence of a mid-Pacific continent instead of the occurrence of long-distance dispersal, but 'there is no evidence for the existence of a 'lost' or sunken mid-Pacific continent' (Carson and Clague, 1995). Tracing the Hawaiian chain backwards to the Emperor Seamounts and their predecessors closer to Asia doesn't even offer steppingstones between Asia and the present-day Hawaiian flora: 'Following the formation of Koko Volcano in the southern Emperor chain about 48Ma, no islands higher than 1,000 m formed until Kure about 29Ma. By the time Kure formed, all the previous high islands had subsided' (Carson and Clague, 1995; Clague and Holcomb, 1995). Pacific volcanic islands other than the Hawaiian chain offer equally potent refutations of vicariance biogeographic methods.

In retrospect, vicariance biogeography appears to be, as McDowall (1976) states, simpl-

Darlington, etc., in analyzing continental distribution patterns in relation to geological events. Vicariance biogeography is of no assistance in analyzing patterns involving long distance dispersal. In fact, the strongest evidence to date needed for biogeographic analysis of all patterns has come from DNA studies utilizing cladistic analysis. The powerful nature of molecular evidence has superseded vicariance methods, which can at best offer results rather vague in comparison with the best molecular methods (especially when more than one DNA site or one type of molecular evidence is studied). Molecular evidence is applicable at all levels of differentiation from population to phylum.

To date, cladistic formulation of molecular evidence (sometimes with the addition of morphological data to the cladograms, sometimes with morphological data plotted separately) has primarily expressed results in terms of phylogenies of taxonomic groups. However, as shown by the authors in the Wagner and Funk (1995) volume, area cladograms that show sequences of island occupations for a particular taxonomic group can easily be derived from the taxonomic cladograms. Molecular evidence, as we will see, validates the existence – and even details of – long distance dispersal in a powerful way. Unlike vicariance biogeography, molecular results are equally adept at elucidating patterns that result from tectonic plate movement, and it can help us differentiate between then two types of geographic movement of any particular taxonomic group in remarkably effective ways.

Scenarios and examples

Pacific patterns

The silversword alliance (*Dubautia, Argyroxiphium*, and *Wilkesia* of the Asteraceae) is unusual among taxa on Pacific islands in that origin of this group has not been traced to Indomalesian ancestors. Fosberg (1948) regarded the geographic affinities of the alliance under his category 'Obscure,' but anatomical evidence (Carlquist 1959a, 1959b) clearly indicated the silversword alliance was derived from the California tarweeds (tribe Heliantheae, subtribe Madiinae). Anatomical evidence may not seem highly persuasive by itself, but several categories of molecular evidence on the group have now been analyzed (Baldwin *et al.*, 1990; Bald-

notably *Raillardiopsis* and *Madia*. The only remnant question is whether the basal genus, *Argyroxiphium*, separated from the *Dubautia–Wilkesia* line on Kauai or on a pre-Kauai island (Baldwin and Robichaux, 1995); I tend to favor Kauai from evidence presently available (Carlquist, 1995). A hybrid between *Raillardiopsis* (California) and *Dubautia* has even been made (Bruce Baldwin, personal communication); F[1] seedlings were readily obtained, but they are not fertile. Thus, dramatic evidence for dispersal of a *Raillardiopsis*-like ancestor from montane northern California to Kauai or a pre-Kauai island – across at least 3,900 km of unbroken expanse of ocean with no intervening stepping-stone islands occurred probably no earlier than 5Ma. The power of molecular evidence in demonstrating with such a high degree of statistical likelihood the dispersal history of the tarweed entry to the Hawaiian chain and then, as adaptive radiation occurred, dispersal of the complex within the chain, is overwhelming, especially when the agreement between more than one line of molecular evidence and the anatomical evidence is so close. However, the precision and clarity of these methods are by no means unique.

Tetramolopium, a genus of Asteraceae, tribe Astereae, offers an example with a dispersal history quite different from that of the silverword alliance (Lowrey, 1986, 1995; Lowrey and Crawford, 1985). Evidence clearly shows dispersal of *Tetramolopium* from New Guinea to the Hawaiian chain, but to one of the newer islands of the pressent-day chain rather to an older island. *Tetramolopium* arrived on one of the islands of the 'Maui-nui' complex (Lanai, Maui, Molokai: the volcanoes of these islands were once coalescent with each other). From 'Maui-nui,' *Tetramolopium* radiated, forming new species, onto Oahu (but not Kauai) and onto the island of Hawaii. The most spectacular dispersal event in the genus after arrival on Maui-nui has been the dispersal of a rather recent Maui and Molokai species, *T. sylvae*, to Mitiaro in the Cook Islands, a distance of approximately 4,300 km. Although the Mitiaro plants are still conspecific with the Hawaiian plants, they are already beginning to differentiate into several lines. The dispersal of *T. sylvae* to Mitiaro is thought to be the result of the ability of the sticky bases of the fruits (or else the pappus bristles) to adhere to the feathers of the Pacific Golden Plover (Lowrey, 1995). There is at

event from New Guinea to Maui-nui. There may have been a different pattern of dispersal routes of birds earlier, and one cannot yet rule out the possibility of travel of the relatively small, light fruits of *Tetramolopium* in the jet stream (alpine origin of Hawaiian *Tetramolopium* is indicated by Lowrey, 1995, and fruits of a high-montane plant might resist the coldness and dryness of the jet stream). We must admit that we have few ideas how bird migratory routes have changed over time. When analyzing the dispersal routes of plants, we tend to assume that all conditions were exactly as they are at present, even though we know that cannot have been true. However, the patterns of dispersal to oceanic volcanic islands in the Pacific are so recent (judging from the data in the Wagner and Funk, 1995, volume: origin for very few groups is hypothesized for a pre-Kauai island) that change has not been drastic since the times when most groups on Pacific volcanic islands dispersed.

The other chapters on Hawaiian plants in the book by Wagner and Funk (1995) give abundant evidence of rapid evolution and diversification, but the biogeographic lessons should not be forgotten. No Hawaiian plant group can be claimed to have colonized an island older than Kure (when it was a high island) because of the pre-Kure pause in island building, mentioned earlier. Thus, colonizations of other Pacific islands that appear similar to the Hawaiian groups in degree of speciation and divergence from ancestors are likely equally recent. The main products of rapid evolution and diversification appear mostly to be present in the Hawaiian flora, with relatively little extinction. This suggests that most of the dispersal to the Hawaiian chain has taken place in the last five million years, with probably extremely few 'relicts' (10Ma or less) from pre-Kauai islands (Kure to Nihoa) playing a conspicuous role in the present-day flora. Dispersal to the Hawaiian chain appears not to have been difficult if the colonizations have mostly been as recent as the molecular evidence suggests.

The vast majority of the plant genera on which intensive studies are reported in the Wagner and Funk (1995) volume are, in fact, probably bird dispersed. The only likely exceptions are the malvaceous genera *Hibiscadelphus* and *Kokia*, which I hypothesized (Carlquist, 1974) might have arrived by rare drift events, because the seeds of many Malvaceae are resistant to salt water although they do not float. The

fact that the genera analyzed by the Wagner and Funk (1995) authors are mostly bird-dispersed is cited at this point because dispersal of plant disseminules by birds either externally or internally has been more difficult for biologists to regard as probable than have the other methods of dispersal. If molecular evidence, when added to other evidence, validates numerous instances of bird-mediated dispersal, molecular evidence has been effective in raising long distance dispersal from a hypothetical process closer to certainty.

Two-ocean patterns

Dispersal that has taken a phylad from one source area to a Pacific Island and to an island in another ocean as well is worthy of attention, because these patterns are so easily misunderstood. For example, Cronk (1992) claims that *Petrobium* (Asteraceae), a monotypic St. Helena I. tree, is a relict with a history of at least 10 million years on St. Helena, and he notes a resemblance to *Oparanthus*, a genus of southeastern Polynesia. The implication is that Petrobium is part of an old pattern, and that both genera are island relicts that have had a history on continental areas. In fact, both *Oparanthus* and *Petrobium* are recent derivatives of *Bidens*, a genus well represented in the eastern Pacific thanks to ease of adherence of fruits to feathers (Carlquist and Pauly, 1985). The relationship of *Bidens* to the two genera is so close, in fact, that Stuessy (1988) has quite justifiably reduced both genera to *Bidens*. Two dispersal events of *Bidens* (very likely beginning with two separate *Bidens* populations) are the best explanation for origin of the *Bidens* species formerly included in *Oparanthus* and *Petrobium*. South American *Bidens* species could have been the source for both, or the Polynesian species could have come from a South American *Bidens* ancestor while the species on St. Helena I. could have come from an African *Bidens*. Eventually, molecular evidence can likely permit us to choose between these alternatives, and to demonstrate how recent the derivations were. The features by which the '*Oparanthus*' and '*Petrobium*' species of *Bidens* differ from their ancestors in the genus are undoubtedly autochthonous island innovations, in view of the patterns in *Bidens* as a whole, rather than happenings on a continent, as Cronk (1992) infers.

McDowall (1976) cleverly cites the distribu-

well as an Atlantic Island, Gough, as an example of a pattern that could be wrongly interpreted as 'another pan-austral Gondwanian pattern.' He cites this example because there is observational evidence (Sykes and Godley, 1968) that seeds of *Sophora* float readily, have been deposited on beaches distant from known native sites (Kermadec Islands), and can germinate after soaking for three years in seawater.

Another two-ocean distribution is represented by two closely related *Acacia* species: *A. koa* of the Hawaiian Islands and *A. heterophylla* of Mauritius. Seeds of *A. koa* do not float. Very likely both species stem from an Australian *Acacia* in which unopened pods or branches float, but seeds do not, or possibly an Australian *Acacia* in which seeds once floated but in which seed flotation ability has been lost during evolution on the island. *Acacia simplicifolia* (Samoa, Tonga) has pods (legumes) segmented into watertight compartments, each containing a seed, and this mechanism explains how this species arrived on Samoa and Tonga even though seeds of *A. simplicifolia* do not float: these features may be somewhat like those of the ancestors of *A. koa*.

Intercontinental dispersal

The evidence of intercontinental dispersal patterns is not directly relevant to instances of dispersal to Pacific oceanic islands. However, the distances involved are often great, particularly in the California-Chile disjunctions, and dispersal to oceanic islands look almost easier to explain (except for the presence of well-known bird flyways that interconnect the disjunct sites). Because instances of intercontinental dispersal depend on birds as dispersal agents, and because dispersal by birds is the type that has aroused the most skepticism, study of instances of intercontinental dispersal should be integral to study of dispersal to oceanic islands. Only a few examples of this literature can be cited, but the reader is referred to the following papers and the important references they cite: Carlquist (1983), Dunn (1971), Porter (1974), Solbrig (1972), Turner (1972), Wells and Hunziker (1976), and Wickens (1976). Although much of this literature is not recent, it is still valid. Lack of recent studies relative to bird dispersal may be related to cessation of methods considered excessively destructive and therefore unacceptable

In the past three decades, significant contributions have been made to our understanding of long distance dispersal. Wallace (1880, p. 73) cites an occurrence in which a boa constrictor (which had to originate either from South America or Trinidad) was seen floating ashore on a log on the island of St. Vincent; the boa actually landed successfully and was then killed. Observations of such bona fide events of long distance dispersal are rare, perhaps only a few per century, and we cannot reasonably expect the number of such observations to increase. However, the majority of our understanding of long distance dispersal comes from 'normal' or short distance dispersal, and we definitely can observe these happenings readily. Moreover, we can do experimental work that can show if the mechanisms for short distance dispersal can work over long distances (*e.g.*, can seeds lodged in bird feathers stay there despite prolonged shaking?). And we can strengthen the circumstantial evidence for long distance dispersal enormously by evidence with high degrees of statistical likelihood, such as is now being provided by molecular evidence analyzed cladistically. These advances may not convert those few who are unusually skeptical about the efficacy of long distance dispersal modes. As a way of placing these modes into relief, a graphic summary (Fig. 1) of means of dispersal to particular Pacific Islands is presented. This figure is reproduced from Carlquist (1974). The method for construction of this figure was first to estimate for each island or island group the minimum number of propagules necessary to account for the native flora. For example, the silversword alliance of the Hawaiian chain was considered derived from a single dispersal event. Then each hypothetical dispersal event was assigned to one of the seven dispersal categories in the Key glyph (Fig. 1, lower left), and the number in each of these categories for a particular island or island group was computed as a percentage of the total number of hypothetical immigrants (N).

Air flotation

Flotation of seeds or small fruits in air currents accounts for a very small proportion of floras of high islands, and 0% on atolls. The highest percentage of arrival by air flotation is on San Clemente I, which is rather close to the California coast, and the plants in this category are strongly distance-dependent (all dispersal mechanisms are distance-dependent, but some are much more strongly so when compared to others). The next highest percentage in the Pacific is on Samoa; most of the plants in this category on Samoa are orchids. The distance to Samoa from source areas (*e.g.*, Fiji) is relatively small, whereas to arrive on the Hawaiian chain, seeds must travel much longer distances. To travel distances of this sort, travel in the jet stream is necessary, but the jet stream is very cold and dry because it occurs at high elevations and such extreme conditions are lethal to seeds of orchids. Lower altitude storm systems might have brought air-floated seeds across the distances between Samoa and its source areas. This possibility of anemophily for very small seeds is validated by the experimental work of Corn (1972), who found that *Metrosideros* seeds survived −30 C. for at least six hours and soaking in seawater for 30 days. These are unusual capabilities for such small seeds, but are requisites for an airborne seed that is likely to reach such a distant high island as any of the Hawaiian chain from a South Pacific source area. Very likely temperate orchids have seeds that withstand cold and dryness better than tropical orchids, and the Hawaiian orchids are temperate (*e.g.*, *Habenaria*), whereas Samoan orchid genera are typical of tropical areas.

Air flotation is effective for seeds and fruits traversing continental areas because propagules can be lofted from the ground surface repeatedly, so shorter air flotation times per lofting episode can suffice (Maddox and Carlquist, 1985). The end of a lofting episode is fatal where overwater travel is concerned. On Surtsey, the minute fruits of one species of flowering plant (*Eriophorum*, Cyperaceae) were actually observed to arrive from Iceland by means of air flotation (Fridriksson, 1975). *Eriophorum* is unusual in its family in having very small fruits attached to abundant fluffy appendage hairs, so that air flotation of *Eriophorum* across the moderate distance that separates Surtsey from Iceland is comprehensible. For long distances, however air flotation of seeds or fruits is relatively ineffective except for a few species. Thus, I have hypothesized long distance transportation of pappose fruits of Asteraceae to islands attached to bird feathers rather than by the parachute-like action that would disperse them in wind gusts on continental areas (Carlquist, 1974).

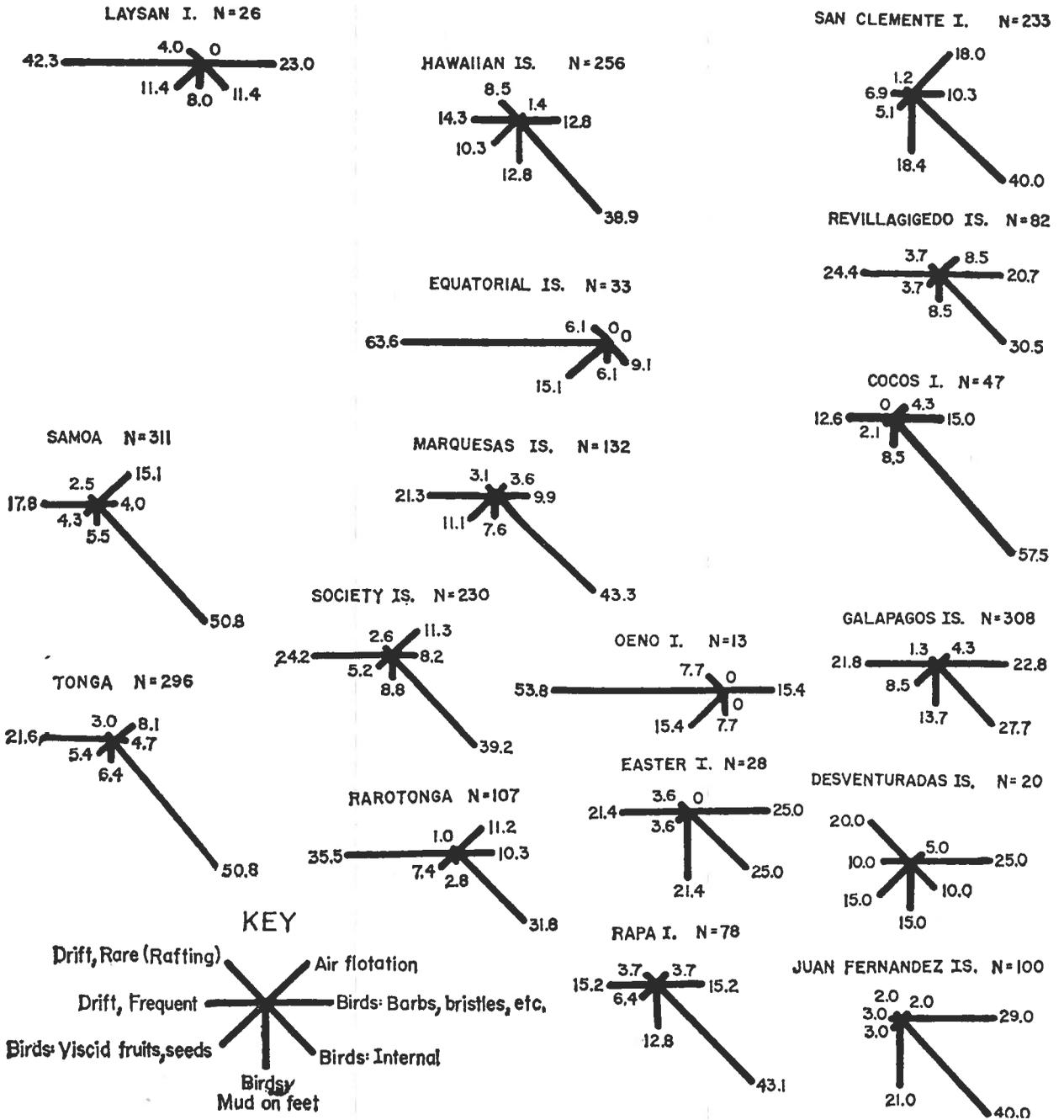Obviously, flotation in air is much more effec-

Fig. 1. Schematic representation of modes of arrival, based on hypothetical immigrants, that would account for present-day native floras, for islands and island groups of the Pacific. Key to dispersal methods at lower left; length of bars in 'glyphs' represents relative proportion of particular dispersal methods (percentages also given). Glyphs representing islands and island groups are arranged according to geography, but distances among them are not proportional to the actual spaces between the islands. For further explanation of how this figure was derived and for extended analyses based on it, see accompanying text. This figure has been published in Carlquist (1967, 1974), and is reproduced with permission of the Bulletin of the Torrey Botanical Club.

The extensive literature on 'aerobiology' focuses mainly on pollen grains, but since spores are in the same size categories (or even smaller than pollen grains), principles in literature on airborne pollen apply to spores as well. One can also hypothesize spore transport in crevices of feather or skin of birds, because anything as small as a spore is very likely to become lodged in textured surfaces. However, anyone skeptical about whether spores (or even small seeds) can travel in jet streams should consult the results of Gressitt *et al.* (1961), discussed in detail below under 'Minute Seeds.'

Seawater flotation

The ease of observation of drift seeds and fruits has led some to overestimate the role of seawater flotation in the populating of oceanic islands with plants. The actual proportion of plants brought by seawater flotation (Fig. 1) is small except for atolls (Equatorial Is.; Oeno) and islands in which inland montane areas are not extensive or richly vegetated (*e.g.*, Rarotonga as compared to Samoa). Islands with small beach areas (San Clemente I., Juan Fernandez Is.) have acquired fewest arrivals by means of seawater flotation events. There is no doubt early arrivals to new volcanic islands chiefly come by seawater flotation, as shown by *Cakile* and *Honckneya* arrivals on Surtsey (Fridriksson, 1975). Entire live plants and viable plant fragments also wash up on shores and take roots, as has been observed on Surtsey (1975).

The plants brought by repetitive events of drift (DF in Fig. 1) appear rarely to evolve into inland areas. The reason appears to be the 'beach syndrome,' in which dispersal by means of flotation and the numerous highly distinctive adaptations of beach plants prevent beach plants from simultaneously (or in rapid sequence) losing the numerous features of this syndrome so that adaptation to inland habitats can occur. The 'beach syndrome' does not appear to be so restrictive in plants brought in rare events of drift (DR in Fig. 1), plants that have one or more features that permit travel in seawater but are not entirely adapted to seawater flotation in the fashion that beach plants are. Such plants might arrive in floating mats of vegetation, or as branches bearing unopened pods, etc. A number of Fabaceae (*e.g.*, *Acacia*, see above) or Malvaceae (*Gossypium*) appear to fall

derived from rare drift events of this sort. Seeds of some Fabaceae and Malvaceae can germinate after exposure to seawater although the seeds do not float (Carlquist, 1974). Because the plants brought by rare events of drift may owe their arrival to more than one feature, not just resistance to seeds to exposure to seawater, assigning a species to the nonrepetitive drift category is difficult. Examination of plants in this category and development of more information about them is a promising task for future research.

Dispersal externally on birds: barbed or bristly fruits or seeds

Dispersal of seeds and fruits to oceanic islands by birds proves to be much more efficient that has been thought. One reason why is to be found in the close ecological match between source and target areas that birds by necessity of finding similar foods manage. A given migrant bird that has picked up fruits and seeds in a source area is likely to search for food in a very similar habitat of a target area, and thus seeds and fruits transported – even though small in number – tend to be deposited with relatively great frequency in places suitable for their growth. Transport by means of air flotation results in an extremely high proportion of seeds falling on unsuitable localities. Even transport by oceanic drift results in deposition on unsuitable places (*e.g.*, tropical seeds deposited on temperate beaches), and very likely the vast bulk of seeds floating in seawater are not deposited on beaches and ultimately sink. The precision of dispersal by birds to suitable localities undoubtedly compensates for the relatively small biomass of seeds successfully carried by birds. With respect to external transport on birds (barbed or bristly fruits or seeds; viscid fruits or seeds), one need not be concerned with birds that eat fruits, so that marine birds as well as shore birds would be effective.

The various Pacific island floras that feature the highest percentage of barbed or bristly fruits are islands that are relatively dry or have extensive dry areas (*e.g.*, Galapagos, Desventuradas, Juan Fernandez, or Revillagigedo Islands). Bristly fruits are least common in floras where wet forest extends down to the beach, as in Samoa. The fact that drier coastal areas have a higher proportion of barbed and bristly fruits than do wet forest areas means also that migratory birds,

which frequent the coast more than inland areas, are likely to come into contact with, and deposit these fruits, in dry coastal areas. Thus, there is a relatively close ecological association.

Experimental work has shown how firmly barbed or bristly fruits become embedded in fur or feathers (Carlquist and Pauly, 1985). When pressed manually into feathers in these experiments, *Bidens* fruits showed 100% adherence even when the fur or feathers were shaken. Even if simply dropped onto the surface of feathers, 27% of *B. pilosa* fruits became attached so firmly that shaking did not dislodge them. These experiments are important not merely in showing the excellence of the attachment mechanisms, but that once attached, fruits or seeds tend not to become detached, so that this means of transport is comparatively distance-independent.

Dispersal externally on birds: viscid seeds and fruits

Viscid seeds and fruits, carried externally on bird surfaces, are more characteristic of dry forests than of wet forests. However, species with viscid seeds or fruits tend to form a smaller proportion of island floras than do species with barbed or bristly fruits. This very likely is true in the world flora at large, although I know of no figures on this. Species with viscid fruits or seeds range all the way from *Pittosporum*, a dry to mesic forest element, to *Boerhaavia*, a beach element. The percentage of arrivals of viscid fruits or seeds on the Hawaiian Islands is a little higher than it is on other islands. This may be indicative of the fact that other means of transport that are more highly distance-dependent show a fall-off because of great distance to the Hawaiian chain and have provided the Hawaiian chain with relatively fewer immigrants. Thus, dispersal of viscid seeds and fruits externally on birds accounts for a relatively higher proportion of the immigrant species of the Hawaiian chain.

Dipsersal internally in birds

The most important mode of arrival on Pacific high islands is internal transport in birds, in contrast to atolls, where the most important means of arrival is by flotation in seawater (Fig. 1). Rarotonga is an example of an island that is

Rarotonga is a much eroded high island with a depauperate forest; beaches are extensive on Rarotonga. Samoa, Tonga, and Cocos are relatively wet and close to source areas; these three island groups have percentages above 50% for this category. Fruits and seeds eaten by birds are not merely colorful and fleshy, they include nonfleshy brown and green fruits and seeds as well, although the majority of species likely to be transported internally in birds do have colorful fleshy fruits. Fleshy fruits tend to be closely correlated with wet forest areas, so ecology suitable for wet forest favors arrival of fruits or seeds internally in birds. The fact that the percentage of transport internally in birds is lower on the Hawaiian Islands than on Samoa, Tonga, or Cocos is likely related to distance: birds can and do carry seeds internally, but excretion and regurgitation of seeds do occur with time, and since flying time is a function of distance, internal transport of seeds and fruits in birds is moderately strongly distance dependent.

The percentages in Fig. 1 may startle those who believe that internal transport in birds really is not very effective. Skeptics point to the tendency of fruit-eating birds not to be long distance migrators; to the tendency of migratory birds not to frequent wet forests; and to the tendency for seeds and fruits to be excreted quickly or else destroyed by grit in gizzards. All of these 'tendencies' have some validity as generalizations, but exceptions are so numerous that the generalizations are, in fact, not a basis for judgment about the effectiveness of internal transport in birds.

The birds most likely to be effective in internal transport of seeds and fruits to many Pacific oceanic islands are shore birds. The number of species that visit any particular island may not be great, but certainly they do visit islands such as the Hawaiian Islands in large numbers. The number of bird individuals is of greater concern that the number of bird species involved in any flyway where transport of seeds and fruits is concerned. The Pacific Golden Plover, which annually migrates from Siberia and Alaska as far south as Tahiti, is often cited as a potential source for internal transport of seeds and fruits to the Hawaiian Islands and islands south of them. The Pacific Golden Plover is undoubtedly a prime candidate for carrying plant disseminules to these islands, but there are other shore birds that annually arrive in large numbers on the Hawaiian Islands. The idea that shore

large proportion of their diet in the form of marine animals, but an appreciable quantity of their diet is seeds and fruits, and this has been documented on many occasions; moreover, gizzards of shore birds do not crush seeds as effectively as do those of passerine birds (for a review of literature on the preceding points, see Proctor, 1968, and Carlquist, 1983).

Certainly the caged shorebirds studied experimentally by Proctor (1968) – Killdeer and Least Sandpipers – readily ate seeds offered to them. Retention of seeds of seeds for times up to 340 hours was recorded: seeds were ultimately regurgitated. Regurgitated seeds are often reingested, furthering the dispersal possibilities of seeds (Proctor, 1968). The times reported by Proctor (1968) are in marked contrast with the popularly held idea that birds always excrete seeds quickly (Ridley, 1930).

Observations on stomach contents of shore birds arriving on oceanic islands would be valuable, but the necessarily destructive nature of shooting birds or the difficulty of trapping them for study of their contents tends to prevent such studies today. One recent observation on stomach contents of arriving birds, however, was made in connection with the investigations of the recently emergent Icelandic island Surstey (Fridricksson, 1975). Stomach contents of incoming snow buntings belonging to a race not native to Iceland were examined. The stomachs contained *Empetrum*, *Scirpus*, *Spergula*, *Carex nigra*, and *Polygonum persicaria*. The last-named is a species not native to Iceland. The seeds of the *Polygonum* and the *Carex* recovered from the stomachs were planted and were grown into mature plants. The other seeds, however, appeared viable. Instances such as this and the work cited above show that wherever extensive investigations into the possible role of migratory birds in transport of seeds and fruits are undertaken, the evidence for such transport is positive. The fact that such evidence exists and can be estimated in terms of, say, the 10 million years available for the colonization of the present-day Hawaiian chain and its post-Kure precursor islands should be impressive. The percentages for internal transport in birds shown in Fig. 1 do not seem to be unrealistic when these factors are taken into account.

The category reported in Fig. 1 as 'Birds: mud on feet' is really an oversimplification for minute seeds for which there is potentially a wide range of potential distribution methods. The concept of 'mud on feet' as a potential medium for carriage of seeds derives from the example of the mud on the partridge foot examined by Darwin (1859) and cited above, but other substances might adhere small seeds to bird surfaces as well. Certainly tarry and viscid substances are present in the environments of migratory birds, and seeds can adhere to these. Crevices on the relatively textured surfaces of bird skins and feathers could provide sites for lodging of minute seeds. Moreover, when we are dealing with minute seeds about 2 mm or less in diameter (the size that forms the basis for the 'mud on feet' category), transport by flotation in air is not inconceivable. Particles in this size range were taken in the trap used in an airplane by Gressitt *et al.* (1961). For example, they report a granite fragment $1.7 \times 2.5 \times 1$ mm at 1,800 m, and a granite fragment $5 \times 4 \times 2.5$ mm at 3,050 m. In view of these results, some of the small seeds referred to the 'Mud on feet' category could have been included in the 'Air Flotation' category, and shifting them to that category would be justified if these seeds could resist the extreme cold and dryness at jet stream elevations. Travel of minute seeds does not, in any case, seem to offer the problems of credibility that other kinds of transport seem to evoke. The highest percentages for arrival of minute seeds on Pacific islands are found on islands relatively close to continents: San Clemente (18.4), Galapagos Is. (15.7), and Juan Fernandez Is. (21). The relatively high percentages for this category on Rapa and the Hawaiian chain (12.8 on each) may relate to the great distance of these from source areas, because the capacity for travel of minute seeds, whether embedded in mud or other substances, in crevices on bird surfaces, or even carried in the jet stream, are less distance-dependent than are the other modes of transport.

Concluding remarks

Those who are skeptical that long distance dispersal is a sufficient explanation for populating the volcanic islands of the Pacific with plants and animals are relatively few, although the validity of an idea in science is not determined by

a democratic vote at a given time. However, the past three decades have brought information that greatly enhances the possibility that the mode of transport about which most commentators are skeptical – internal transport of seeds in birds – is quite likely, thanks to the results of (Proctor, 1968), and the realization that the literature contains more positive information on stomach contents of shore birds than has hitherto been appreciated. The visits of shore birds to oceanic islands are now being recorded in a much more detailed and verifiable fashion than in earlier years because more workers and more precise methods are now involved in accumulation of records.

Where circumstantial evidence on long distance dispersal is concerned, evidence is becoming extraordinarily strong thanks to the very high degree of likelihood that assemblage of various kinds of molecular data can give to a cladistically constructed phylogeny. The story of the silversword alliance (Hawaiian tarweeds), detailed above, is surely undeniable, and is one of the most dramatic stories yet developed in evolutionary biology. We can now claim with a high degree of certainty that a single event of dispersal occurred by means of external attachment to a bird – probably a shore bird – of a fruit of a tarweed taxonomically close to *Raillardiopsis*, growing in montane northern California. The transport event led to establishment of the tarweed on alpine Kauai (or possibly a pre-Kauai island) and was followed by the radiation of the tarweeds into an amazing range of growth forms and habitats, involving intricate anatomical and physiological adaptations, as well as further dispersal events within the Hawaiian chain, dispersal events that can be well documented on the basis of now-available molecular and other data. The development of the massive evidence for this single (although large) evolutionary story has certified the existence of long distance dispersal to a remote island. In addition, the possibility of developing such a story invites us to present stories of other plant and animal groups with comparable detail and degree of confidence, so that our knowledge of plant dispersal in the Pacific is now likely to accelerate.

References

Baldwin, B.G., Kyhos, D.W. and Dvorak, J. 1990. Chloroplast DNA evolution and adaptive radiation in the Hawaiian silversword alliance (Asteraceae-Madiinae). Ann. Mis-

Chloroplast DNA evidence for a North American origin of the Hawaiian silversword alliance (Asteraceae). Proc. Nat. Acad. Sci. 88: 1840–1843.

Baldwin, B.G. and Robichaux, R.H. 1995. Historical biogeography and ecology of the Hawaiian silversword alliance (Asteraceae): new molecular phylogenetic perspectives. *In* Hawaiian biogeography. pp. 259–287. Edited by W.L. Wagner and V.A. Funk. Smithsonian Inst. Press, Washington, D.C.

Ball, I.R. 1975. Nature and formulation of biogeographical hypotheses. Syst. Zool. 24: 407–430.

Carlquist, S. 1959a. Vegetative anatomy of *Dubautia, Argyroxiphium,* and *Wilkesia* (Compositae). Pac. Sci. 13: 195–210.

Carlquist, S. 1959b. Studies on Madiinae: anatomy, cytology, and evolutionary relationships. Aliso 4: 171–236.

Carlquist, S. 1967. The biota of long-distance dispersal. V. Plant dispersal to Pacific islands. Bull. Torrey Bot. Club 94: 129–162.

Carlquist, S. 1974. Island biology. Columbia Univ. Press, New York. 660 pp.

Carlquist, S. 1983. Intercontinental dispersal. Sonderb. naturwiss. Verh. Hamburg 7: 37–47.

Carlquist, S. 1995. Introduction. *In* Hawaiian biogeography. Edited by W.L. Wagner and V. Funk. pp. 1–13. Smithsonian Institution Press, Washington, D.C.

Carlquist, S. and Pauly, Q. 1985. Experimental studies on epizoochorous dispersal in Californian plants. Aliso 11: 167–177.

Carson, H.L. and Clague, D.A. 1995. Geology and biogeography of the Hawaiian Islands. *In* Hawaiian biogeography. pp.14–29. Edited by W.L. Wagner and F.A. Funk. Smithsonian Inst. Press, Washington, D.C.

Clague, D.A. and Holcomb, R.T. 1995. The geography of the Hawaiian-Emperor Island chain. *In* Geology of the U.S. seafloor: the view from GLORIA. pp. n–00. Edited by J. Gardner, M. Field, and D. Twichell. Cambridge Univ. Press, Cambridge.

Corn, C. 1972. Seed dispersal methods in Hawaiian *Metrosideros.* Island Ecosystems IBP, U.S. International Biological Program, Technical Report 6: 1–19.

Cronk, Q.C.B. 1992. Relict floras of Atlantic Islands: patterns assessed. Biol. J. Linnean Soc. 46: 91–103.

Darwin, C. 1859. The origin of species. Original text with preface and introduction. Random House, New York. 689 pp.

Dunn, D.B. 1971. A case of long range dispersal and 'rapid speciation' in *Lupinus.* Trans. Missouri Acad. Sci. 5: 26–38.

Fosberg, F.R. 1948. Derivation of the flora of the Hawaiian Islands. *In* Insects of Hawaii, Vol. 1, Introduction. pp. 107–119. Edited by E.C. Zimmerman. University of Hawaii Press, Honolulu.

Fridriksson, S. 1975. Surtsey. John Wiley and Sons, New York and Toronto. 198 pp.

Gressitt, J.L., Sedlacek, J., Wise, K.A.J. and Yoshimoto, C.M. 1961. A high speed airplane trap for air-borne organisms. Pac. Insects 3: 549–555.

Jensen, R.K., Michaels, H.J. and Palmer, R.D. 1991. Phylogeny and character evolution in the Asteraceae based on chloroplast DNA restriction site mapping. Syst. Bot. 16: 98–115.

Love, A, and Love, D. 1967. The origin of the North Atlantic flora. Aquilo 6: 52–66.

Lowrey, T.E. 1986. A biosystematic revision of Hawaiian *Tetramolopium* (Compositae: Astereae). Allertonia 4:

Lowrey, T.E. and D.L. Crawford. 1985. Allozyme divergence and evolution in *Tetramolopium* (Compositae: Astereae) on the Hawaiian Islands. Syst. Bot. 10: 64–72.

Maddox, J.C. and Carlquist, S. 1985. Wind dispersal in Californian desert plants: experimental studies and conceptual considerations. Aliso 11: 77–96.

McDowall, R.M. 1976. Generalized tracks and dispersal in biogeography. Syst. Zool. 27: 88–104.

Nelson, G.J. 1974. Historical biogeography: an alternative formalization. Syst. Zool. 23: 555–558.

Platnick, N.I. 1976. Drifting spiders or continents? Vicariance biogeography of the spider subfamily Larontinae (Araneae: Gnaphosidae). Syst. Zool. 25: 101–109.

Porter, D.M. 1974. Disjunct distributions in the New World Zygophyllaceae. Taxon 23: 339–346.

Proctor, V.W. 1968. Long-distance dispersal of seeds by retention in digestive tract of birds. Science 160: 321–322.

Ridley, H.N. 1930. The dispersal of plants throughout the world. L. Reeve and Co. Ashford, Kent, England. 744 pp.

Rosen, D.E. 1975. A vicariance model of Caribbean biogeography. Syst. Zool. 24: 431–464.

Skottsberg, C. 1924. Einige Bemerkungen über die alpinen Gefässpflanzen von Masafuera (Juan Fernandez Inseln). Festschr. Carl Schroter, Verh. des Geobot. Inst. Rubeck in Zürich 3: 87–96.

Skottsberg, C. 1928. Pollinationsbiologie und Samenverbreitung auf den Juan Fernandez-Inseln. Nat. Hist. Juan Fernandez and Easter I. 2: 503–547.

Skottsberg, C. 1940. Report on Hawaiian bogs. Proc. Sixth Pac. Sci. Congr. 4: 659–661.

Solbrig, O.T. 1972. The floristic disjunctions between the

Steenis, C.G.G.J. van. 1962. The land bridge theory in botany with particular reference to tropical plants. Blumea 11: 235–542.

Stuessy, T.F. 1988. Generic relationships of *Oparanthus* and *Petrobium*, especially with reference to *Bidens* (Compositae, Heliantheae, Coreopsidinae). Brittonia 40: 195–199.

Sykes, W.R., and Godley, E.J. 1968. Transoceanic dispersal in *Sophora* and other genera. Nature 218: 495–496.

Turner, B.L. 1972. Chemosystematic data: their use in the study of disjunctions. Ann. Missouri Bot Gard. 59: 152–164.

Wagner, W.L. and Funk, V.A. (eds.) 1995. Hawaiian Biogeography. Smithsonian Inst. Press, Washington, D.C. 467 pp.

Wallace, A.R. 1880. Island Life. Macmillan and Co., London. 526 pp.

Wells, P.V. and Hunziker, J.H. 1976. Origin of the creosote bush (*Larrea*) deserts of southwestern North America. Ann. Missouri Bot. Gard. 63: 843–861.

Wickens, G.E. 1976. Speculations on long distance dispersal and the flora of Jebel Marra, Sudan Republic. Kew Bull. 31: 105–150.

Williamson, M. 1984. Sir Joseph Hooker's lecture in insular floras. Biol. J. Linnean Soc. 22: 44–77.

Witter, M.S. 1990. Evolution in the Madiinae: evidence from enzyme electrophoresis, Ann. Missouri Bot. Gard. 77: 110–117.

Witter, M.S. and Carr, G.D. 1988. Adaptive radiation and genetic differentiation in the Hawaiian silversword alliance (Compositae: Madiinae). Evolution 42: 1278–1287.