THE BIOTA OF LONG-DISTANCE DISPERSAL. III. LOSS OF DISPERSIBILITY IN THE HAWAIIAN FLORA

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INTRODUCTION

The Hawaiian flora is ideal for demonstration of phenomena of evolution on oceanic islands because the Hawaiian Islands have a high degree of ecological opportunity, a strong isolation, and a relatively great age, especially when now-vanished.
high islands of the Leeward Hawaiian chain are taken into account. A phenomenon in the Hawaiian flora which has as yet attracted little attention is the tendency for endemic species to show diminution in dispersibility when compared with mainland or continental-island relatives. Estimation of the degree to which dispersibility has been diminished is, of course, difficult, and the interpretations in this paper may be regarded as somewhat speculative. The phenomenon is real enough, however, so that this summary may serve to inspire further and more critical examination of particular cases and further observational and experimental work.

The importance of loss of dispersibility to biogeographical thinking is considerable. There is a tendency for phytogeographers to believe that the present dispersal ability of an island species is the same as that of its ancestral immigrant stock. Dispersal mechanisms are, of course, subject to evolutionary change as are other characters. If one fails to take this into account, the dispersal ability of the Hawaiian flora as a whole appears too low for all immigrant stocks to have arrived across long seawater distances. On the contrary, the Hawaiian flora is one whose component species are all basically adapted to long-distance dispersal, although an appreciable number have lost partly or wholly the dispersal mechanism or ability which brought their ancestors to the Hawaiian Islands.

A phenomenon allied to loss of dispersibility is a lowered rate of fertility, a tendency noted earlier in island faunas and suspected in island floras (Carlquist 1965, 1966a). In some Hawaiian species, the increase in seed size which suggests a lowered dispersal ability is accompanied by the production of fewer seeds, thus lowering the total fertility of a species. As will be seen, a shift in ecological preference can also be expressed in terms of increased fruit and seed size. “Loss of dispersibility,” therefore, may be regarded as a byproduct of various evolutionary changes in the Hawaiian flora, and not necessarily a prime factor which has a strong selective value. As noted earlier (Carlquist 1966b), tendencies which may be designated in this fashion are not limited to oceanic islands, but may be found in certain components of continental floras as well. Lowered dispersal ability can be seen clearly in the Hawaiian flora, however, and is in that context uniquely related to the entire “syndrome” of evolutionary changes which characterize oceanic islands.

The operative factors which result in loss of dispersibility are several and may differ in various cases. They cannot, therefore, be rated as to which is more, which less important in the cases as a whole. One probably important factor may be described as precinctiveness, a tendency noted by Beccari and Rock (1921) in *Pritchardia*. Briefly defined, precinctiveness denotes reproduction in such a fashion that most propagules are shed within a limited zone of stable conditions, such as wet forest, to which a species has a highly specialized ecological adaptation. This permits, potentially, survival of more numerous propagules than would widespread dissemination. One can assume that species may be expected to adjust their reproductive abundance to a rate suitable for occupation of favorable sites. In strand plants and weedy species, reproductive rates may be said to be high because favorable sites are widely scattered and change rapidly. In species of stable forest, a lower reproductive rate would be expected to suffice.

An extreme function of precinctiveness would be the tendency for lowered dispersibility to prevent the majority of propagules from being blown away from an island. Excessive loss of propagules seems unlikely in Hawaiian flowering plants, where most species with lowered dispersal ability occupy not windy sites, but relatively protected sites in forests. Likewise, wind pressure seems insufficient to explain development of flightlessness in Hawaiian insects (Perkins 1913). Wind pressure is, however, a very real factor for plants with very small propagules, such as ferns.
A second probable factor in loss of dispersibility is the tendency for immigrants to oceanic islands to be originally "weedy" plants, capable of establishing in pioneering conditions, and for these immigrants then to evolve characteristics of stable forest species (Carlquist 1965, 1966a). The continental forest is characterized by relatively poor dispersal not only because forest trees tend to have large seeds (the abundant storage tissue suited to growth of seedlings in shady forest floors) but also because forest trees may be expected to show a high degree of ecological specialization, so that they would be poor candidates for establishment in pioneer situations. The evolution of Compositae on oceanic islands from herbaceous, weedy ancestors into shrubs and trees of forest regions is a prime example (Carlquist 1966b); this ecological shift is possible under insular conditions because wet forest is a relatively uncontested zone, a fact related to the few wet-forest-species propagules brought to an island by long-distance dispersal. Increase in fruit and seed size is an adjustment to this change in ecological preferences, and loss of dispersibility occurs as a byproduct.

A third possible factor can be described as a failure to maintain the dispersal mechanism which brought an original stock of immigrants to an oceanic island. An example of this tendency was described earlier in the case of Bidens (Carlquist 1966b). The Pacific insular species of Bidens which have the best dispersal mechanisms and appear most similar to ancestral types live on bird cliffs. This suggests that attachment of fruits to bird feathers was the vector for their immigration, and that ancestral species occupied sites where marine birds typically nest. As a species evolves into an upland site, the contact with the vector is lost, and either the old mechanism is lost or a new mechanism develops, or both may occur. If the dispersal mechanism is merely lost, this may be attributed to progressive evolutionary loss of a structure with which a function is no longer associated. Species which have arrived in the Hawaiian Islands by means of oceanic drift cease to utilize this dispersal mechanism when they evolve into upland sites. Floatability no longer has a strong selective value for such species and might be expected to vanish. Any group which evolves into a new ecological territory (such as forest) where the vector (seawater, seabirds) which brought its immigrant ancestor is no longer present may be said to have lost dispersibility to the extent that propagules no longer come into contact with that vector. Losing of contact with a vector is a byproduct of evolutionary opportunity and ecological shift, which in turn are produced by the disharmonic nature of oceanic island floras.

Loss of dispersibility in the Hawaiian flora must be demonstrated in terms of particular genera. One must not only understand the fruit and seed morphology and current dispersal mechanisms of Hawaiian species; one must be able to infer that of ancestral types. Establishing the identity of stocks ancestral to Hawaiian species is relatively easy in some cases, where a genus with endemic species in the Hawaiian Islands is also represented in the southwestern Pacific and Indo-Malaysia. In other cases, relationships still are vague. The comments of Hillebrand (1888) on affinities of Hawaiian genera have proved very helpful. With regard to dispersal mechanisms by which ancestral forms reached the Hawaiian Islands, some cases appear clear, while in others more than one possibility must be admitted. Despite the wealth of information offered by Ridley (1930), Guppy (1906) and others, mechanisms of dispersal in most plants are suppositions, based upon the morphology of fruits and seeds compared to those of species for which good observational data are available.

Although Indo-Malaysian relatives now living west of the andesite line in the western Pacific or American relatives now living on the American mainland would seem the best sources for comparison with Hawaiian endemics, species from other
Pacific oceanic islands, such as Tahiti or the Marquesas, seem worthy of comparison. The Hawaiian Islands show loss of dispersibility more prominently than do other island groups (Carlquist 1966b). A secondary center for loss of dispersibility is represented in Samoa, according to the data of the present paper. Lack of native Compositae in Samoa prevented this fact from appearing in my survey of loss of dispersibility in Compositae (Carlquist 1966b).

The greater ecological opportunity and the strongly disharmonic flora of the Hawaiian Islands seem adequate reasons why the Hawaiian Islands should show loss of dispersibility prominently. On a continental island, such as those west of the andesite line in the Pacific, ecological niches are already pre-empted by the large number of resident species, so evolutionary change is buffered. Moreover, dispersibility retains a relatively high value in harmonic forests on account of the large number of species competing within a given area. Where attrition of seeds can be expected to be high, fairly large numbers of seeds per plant and (as a corollary) relatively vagile propagules may be expected. The size of seeds in these forest trees of harmonic areas may be a compromise between dispersibility and the large-seeded habit typical of forest trees. The value of vagility is lowered in immigrants to the Hawaiian Islands, and with greater ecological opportunity provided by the small number of resident groups there, immigrant stocks are “released,” so these trends can be fulfilled to a much greater extent than on continental islands.

Stages in loss of dispersibility within particular Hawaiian groups are featured in the examples given below. The fact that such series are present suggests that some genera are in a state of transition with respect to loss of dispersibility, and the end-products of such adaptations are not exclusively present.

In an earlier paper (Carlquist 1966b), Compositae were selected for demonstration of loss of dispersibility largely because that family is plastic in an evolutionary sense and is well represented in the eastern Pacific. In that case, islands and island groups represented replicate sites for evolution of poorer dispersibility, and served in the fashion of experimental controls. In the present paper, the various taxonomic groups in the Hawaiian flora serve similarly, for if loss of dispersibility is part of the evolutionary curriculum in floras of ecologically rich oceanic islands, it should characterize many taxonomic groups independently.

Adaptations for long-distance dispersal basic to the Hawaiian flora may be outlined briefly. Dispersal by wind can be supposed for spores of ferns and very minute seeds of flowering plants (orchids, Schiedea, Lobelia). Minute seeds can equally well be supposed to have been transported in mud on feet or feathers of birds, however. Transport externally on birds can be presumed for fruits or seeds with hooks or barbs (Bidens, Acaena, Sanicula) or for seeds or fruits with adhesive coatings (Euphorbia, Pittosporum, Plantago, Pisonia). Minute seeds embedded in a fleshy pulp and eaten by birds (Cyanea, Clermontia, Labordia, Vaccinium) may be transported either externally on feathers or internally in birds. Drupes or berries with seeds of moderate size probably arrived on the Hawaiian Islands mostly through internal transport by birds. One may suspect from the present size of fruits in Hawaiian Rubiaceae, Myrsinaceae, etc., and the similar sizes of fruits in those families on continental areas that the maximum size of fleshy fruit eaten by birds is about 1 cm in diameter, with seeds ca 8 mm or less in diameter. The majority of Hawaiian forest species appear to have had such fruits at the time their ancestral stocks immigrated. Some Hawaiian plants have shiny black seeds which are not accompanied by fleshy pulp but which are of a sort attractive to seed-eating birds (Rutaceae, for example). Flotation by seawater would be expected to have been the vector for a number of Hawaiian species, particularly those of the low or coastal forest. Although the pro-
portion of species in the montane flora of oceanic islands which derive from oceanic drift might be expected to be small, this element appears appreciably larger in the Hawaiian flora than in floras of other oceanic islands. Guppy (1906) has underestimated the importance of oceanic drift as a means of populating oceanic islands. Guppy emphasizes a "Fijian difficulty," whereby coastal strand plants fail to evolve into forest sites, and the reverse also does not occur. For this reason, Guppy seems reluctant to acknowledge the existence of ecological shift from strand to forest in the Hawaiian flora. One should note that Fiji, although insular, retains an essentially continental (harmonic) flora, whereas the Hawaiian flora is strongly disharmonic. In Hawaii, immigrant groups were offered more numerous ecological opportunities, opportunities which would have already been pre-empted on Fiji by the many and varied genera native there. Hawaiian groups (other than those which are currently exclusively strand plants) which may be suspected of having immigrated via seawater include all the native Leguminosae and Malvaceae, at least some Apocynaceae, and the native species of Colubrina, Dodonaea, Gouania, Haplostachys, Myoporurn, Peucedanum, Planchonella, and Pritchardia.

For spores or seeds suspected of being dispersed by wind or in mud on feet of birds, evolutionary increase in size would curtail dispersibility. Adherent fruits would be less likely to be dispersed if barbs or hooks are lost, sticky coatings disappear, or if increase in fruit or seed size makes the adhesive mechanism less likely to be effective. Fleshy fruits and shiny black seeds would lose dispersibility if a larger size made them less readily sought and eaten by resident birds. Seawater-dispersed fruits and seeds would lose dispersal ability if evolutionary change results in eventual loss of floatability—a definitive loss of dispersibility. Increase in size is no hindrance to seawater flotation, but it does lower rate of transport across land areas. A feature worthy of note for types of transport other than oceanic drift is that only a slight decrease in transportability would markedly increase the precinctiveness of a species. This is particularly true in the case of wind-dispersed seeds or spores.

The cases which have been selected for presentation below represent, in my opinion, readily apparent instances of loss of dispersibility. More detailed statistical treatment of other cases would probably reveal additional valid examples.

MATERIALS AND METHODS

Data and observations given below were derived both from material collected in the field and from specimens studied in the herbarium. Living materials were studied wherever possible. The following individuals deserve special credit for aiding my field work during several visits to the Hawaiian Islands: Dr. Warren H. Wagner, Jr., Dr. George W. Gillett, Dr. Harold St. John, and Dr. Elmo C. Hardy. For herbarium studies, the facilities of the Bernice P. Bishop Museum proved indispensable, and I am indebted to Dr. Roland Force and the late Miss Marie Neal for their assistance. The data on fern-spore sizes were collected by Dr. Warren H. Wagner, Jr. under the auspices of a National Science Foundation Grant, GB-2025.

Because this paper is of a theoretical, rather than revisionary nature, full nomenclatural citation and collection data of specimens examined are not given. A list of these has been prepared, however, and is available upon request.

Experiments to determine floatability of seeds and fruits were undertaken, following the methods of Guppy (1906). Such tests were considered valid only if seeds contained normal embryos, and if seeds or fruits either sank immediately or floated for prolonged periods. Tests to determine viability of seeds exposed to salt water were not undertaken. Also not undertaken were tests on normal viability of seeds in
Hawaiian forest species. Both types of tests would be valuable in future studies of the Hawaiian flora.

In the illustrations, scales of magnification are consistent within families, although different from one family to another. Sources of non-Hawaiian species are indicated in parentheses. All species for which no source is cited in the drawings are endemic to the Hawaiian Islands.

FERNS

Dr. Warren H. Wagner, Jr. has kindly contributed data on spore size, ecology and nomenclature of Hawaiian ferns. A selection from this data is given in Table 1. Data on spore-size in non-Hawaiian Schizaeas is from Brown and Brown (1931) and from Selling (1946). Data on the fossil Schizaeas (S. skottsbergii and S. skottsbergii var. mauiensis) are from Selling (1946). Selling’s measurements are apparently uniformly too large by a factor of about 10% and have been corrected in accordance with Wagner (pers. comm.). Spore sizes represent an average of the greatest dimensions of spores from one or more collections. Exotic ferns have been added to the table where, in a given family, there are no Hawaiian representatives in low forest, and a general picture of typical spore sizes in a family is necessary for comparison with species of wet Hawaiian forest.

The examples given in Table 1 indicate a clear correlation between ecology and spore size. Because average size in most fern spores centers around 30 μ, the dimensions of the spores in the wet forest species is truly exceptional. This may be regarded as a specialization with reference to wet forest except in Athyrium, where the small spored A. molokaiense may represent the reverse adaptation to dry lowland conditions. Hawaiian species of Cibotium (Cytatheaceae) are not included in the table. These species do have notably large spores (C. chamissoi, 54.6 μ; C. glaucum, 49.3 μ; C. st.-johnii, 46.5 μ; C. splendens, 52.2 μ). This large spore size characterizes not merely Hawaiian Cibotiums, however, but all Cibotiums. The genus is adapted to wet forest almost uniformly, and thus both Hawaiian and non-Hawaiian Cibotiums may be said to show correlation between wet forest habitat and large spore size.

The explanation for the good correlation shown in Table 1 seems chiefly one of precinctiveness: the large spores of wet forest species will fall nearer the parent plant and will be more likely to survive, for this specialized habitat is quite limited in geographical extent. Although the ferns listed in Table 1 represent a selection from the Hawaiian fern flora, no cases which definitely run counter to the trend of increasing spore size in wetter areas can be said to exist. There are large groups of native ferns which show in spore size neither a positive nor a negative correlation with forest ecology. These mostly Aspleniaceae, Polypodiaceae, and Grammitidaceae—have spores which range mostly between 30 and 45 μ. Significantly, these ferns are almost all epiphytes, whereas the ferns listed in Table 1 are terrestrial. The epiphytic habit represents occupancy of an “open habitat,” one which is widely dispersed. Small or medium-sized spores seem better adapted by virtue of their vagility to reach the many and highly scattered sites suitable for growth of epiphytes. Trees bearing epiphytes are limited in life-span, suggesting another reason for vagility of spores of epiphytic ferns.

Polyploidy and apogamy do influence spore size, of course. None of the ferns listed in Table 1, however, are known to be apogamous, nor do chromosome numbers form a good correlation with the spore-size trends of Table 1 (Wagner, pers. comm.). Indeed, according to Dr. Wagner, the endemic Hawaiian ferns, among which the high-forest species may be cited, tend to be diploid, whereas wider-ranging native
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<tr>
<th>FAMILY</th>
<th>SPECIES OF LOW FOREST, OR WIDESPREAD SPECIES</th>
<th>SPECIES OF INTERMEDIATE FOREST</th>
<th>SPECIES OF HIGH, WET FOREST</th>
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<tbody>
<tr>
<td>Schizaeaceae</td>
<td><em>Schizaea dichotoma</em> (Old World Tropics), 60 µ</td>
<td><em>Vandenboschia draytoniana</em>, 48.6 µ</td>
<td><em>Schizaea skottsbergii</em>, 100 µ</td>
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<td><em>Schizaea digitata</em> (Old World Tropics), 42 µ</td>
<td><em>Goniocorpus minutus</em>, 53.4 µ</td>
<td><em>S. s. var. mauliensis</em>, 90 µ</td>
</tr>
<tr>
<td>Gleicheniaceae</td>
<td><em>Dickranopteris emarginata</em>, 32.4 µ</td>
<td><em>Vandenboschia davalliana</em>, 41.4 µ</td>
<td><em>Sticherus owyhenensis</em>, 36.9 µ</td>
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<td><em>Dickranopteris linearis</em>, 28.7 µ</td>
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<td><em>Hicriopteris pinnata</em>, 26.3 µ</td>
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<td>Hymenophyllaceae</td>
<td><em>Vandenboschia cyrtotricha</em>, 38.4 µ</td>
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<td><em>Vandenboschia davalliana</em>, 41.4 µ</td>
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<td>Adiantaceae</td>
<td><em>Microlepia spelunca</em>, 26.1 µ</td>
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<td><em>Pellaea ternifolia</em>, 41.1 µ</td>
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<td><em>Pityrogramma calomelanos</em> (New World Tropics), 40.3</td>
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<td><em>Pteris excelata</em>, 42.9 µ</td>
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<td><em>Pteris vitata</em>, 34.8 µ</td>
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<td>Blechnaceae</td>
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<td><em>Doodia kunthiana</em>, 39.2 µ</td>
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<td><em>Doodia lyoni</em>, 40.9 µ</td>
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<td>Aspidiaceae</td>
<td><em>Athyrium molokaiense</em>, 36.4 µ</td>
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<td><em>Rumohra adiantiforme</em> (New Zealand), 32.2 µ</td>
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<td><em>Rumohra aristata</em> (Michigan), 33.4 µ</td>
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<td><em>Rumohra hispida</em> (New Zealand), 37.0 µ</td>
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<td><em>Sadleria cyatheoides</em>, 49.6 µ</td>
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<td><em>Sadleria squarrosa</em>, 62.0 µ</td>
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<td><em>Sadleria pallida</em>, 48.9 µ</td>
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<td><em>Sadleria soulejeitiana</em>, 46.9 µ</td>
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<td><em>Athyrium mepianum</em>, 42.6 µ</td>
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<td><em>Athyrium microphyllum</em>, 36.4 µ</td>
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<td><em>Athyrium sandwichianum</em>, 40.3 µ</td>
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<td><em>Rumohra carvolia</em>, 58.8 µ</td>
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fern species in the Hawaiian flora contain the bulk of the species in which Dr. Wagner has now established the existence of polyploidy. The explanation for larger spore sizes in the Hawaiian fern flora seems clearly related to ecology, therefore.

Another noteworthy feature which Dr. Wagner has established for Hawaiian ferns is the exceptional degree to which they possess paraphyses in sori. Although the functions of paraphyses and the reasons for abundance of these structures in Hawaiian ferns cannot be elucidated at present, paraphyses might have the effect of hindering free discharge of spores, and might thereby increase precinctiveness of ferns which possess such paraphyses.

**DICOTYLEDONS**

**Apocynaceae:** Among Hawaiian Apocynaceae, only the endemic genus Pteralyxia suggests a fruit size possibly greater than that of ancestral types. Unfortunately the relationships of Pteralyxia have not been clearly established as yet. Hillebrand (1888) claimed affinity with the American genus Vallesia, whereas Schumann (1895) emphasized resemblances to the wide-ranging Pacific genus Alyxia. The single-seeded drupes of Alyxia do show a close resemblance to those of Pteralyxia in features such as the large locule, filled with ruminate endosperm. Fruits of Alyxia do not float and are probably, because of fleshy exocarp and relatively small size, dispersed by frugivorous birds. Fruits of Pteralyxia, on the other hand, are fusiform and much larger—ranging from about 5 × 2 × 2 cm in P. kauaiensis to about 6 × 4 × 3 cm in P. macrocarpa. This large size would seem clearly to preclude bird dispersal, despite the fleshy exocarp. If Pteralyxia is, in fact, related to Alyxia, this would constitute a remarkable case of loss of dispersal mechanism. On the other hand, dried fruits of Pteralyxia are capable of floating indefinitely, either with or without the fleshy exocarp. This feature is found in such Apocynaceae as Ochrosia oppositifolia (= O. parviflora), a widespread species of the Pacific which is, very likely, seawater-dispersed. Ochrosia sandwicensis, a Hawaiian endemic, probably stems from seawater-dispersed ancestors like O. parviflora, a possibility conceded even by Guuppy (1906). If Pteralyxia is, in fact, related to seawater-dispersed ancestors, there may be relatively little loss of dispersibility, although seeds of Pteralyxia might be rendered inviable by soaking in seawater. Indeed, the woody endocarp is relatively thin and fragile, especially at the peduncle end. The large size of fruits of P. macrocarpa suggest difficulty of transport on land, in any case. Pteralyxia remains one of the few instances about which little can be said with regard to dispersal; information about its relationships is very much needed.

**Araliaceae:** Among Hawaiian Araliaceae, an almost classical case of loss of dispersibility is furnished by the genus Tetraplasandra. The remainder of Hawaiian Araliaceae have drupes of relatively small size, suggesting ease in dispersal by frugivorous birds. Within the Hawaiian species of Tetraplasandra, however, a trend toward marked gigantism of fruits and seeds is evident (Fig. 1). Of the species recognized by Rock (1913) or Sherff (1955), most have fruits which range from 7–10 mm in length. Fruits of these species are characteristically fusiform and ca 8 mm long. Typical of these is T. oahuensis (Fig. 1). This fruit size seems clearly ancestral among Hawaiian species, for it is shared by the non-Hawaiian species of Tetraplasandra: T. philippinensis (Palawan, Philippine Is.: Fig. 1), T. paucident (New Guinea), and T. koerdersii (Celebes). Hawaiian species with slightly larger fruit size include T. hawaiiensis (10 mm in diameter), T. waiamensis (10–12 mm long, 3–4 mm thick), T. meiandra (13–14 mm long, 5–6 mm thick), and T. kauaiensis (Fig. 1; ca 14 mm in diameter). More marked gigantism in fruits is exhibited by two Kauai species:
T. waialealae and T. waimeae (Fig. 1). Drupes of T. waialealae are fusiform, 25–32 mm long, whereas those of T. waimeae are spheroidal, ca 30 mm in diameter. As shown in Fig. 1, sizes of pyrenes in these species are in proportion to size of fruits. There seems clearly to have been a trend toward gigantism in Tetraplasandras with relation to the upper wet rain forest. The two species with the largest fruits are native to high forest of Kauai.

Caryophyllaceae: The Hawaiian endemic genus Schiedea would seem to retain at least in some species the same dispersibility of ancestral types which immigrated to the Hawaiian Islands. Seeds in this genus are most frequently very small and sculptured in various ways which would enhance their adhesion within mud on bird’s feet. Capsules open so that the valves spread widely, providing unimpeded release of seeds. Schiedea globosa (Fig. 2) serves as an example of good retention of dispersibility, as do other lowland species. Exceptions are found in species of somewhat higher altitudes, such as S. amplexicaulis, S. kealiae, and S. diffusa. These species have smooth seeds, which probably disperse slightly less efficiently than the sculptured seeds. This trend is also shown in S. viscosa (Fig. 2) and S. lychnoides, both from mid-altitudes on Kauai. These species not only have somewhat larger seeds than do the other Schiedeas; they have prominent sepals which enfold the capsule at maturity, hindering the release of seeds. This suggests a shaker type of dispersal, in which seeds are disseminated more gradually. Schiedea viscosa and S. lychnoides were claimed by...
Hillebrand (1888) to be transitional to another endemic Hawaiian genus, *Alsinodendron*, and possibly may be included in the latter (Sherff 1944). *Alsinodendron trimervae* (Fig. 2) is notable not only for seeds which are markedly larger than those of *Schiedea*, but also for sepal which enclose the capsule and are fleshy, becoming dark blue at maturity. This suggests a drupe-like structure which might well represent a shift to dissemination by frugivorous birds. Certainly *Alsinodendron trimervae* represents the furthest penetration in this series into a forest habitat, for it grows near the summit of Oahu's highest mountain, Kaala.

**Compositae:** Loss of dispersibility in Hawaiian native Compositae is discussed elsewhere (Carlquist 1966b).

**Convolvulaceae:** The Hawaiian *Breweria menziesii* is notable for its large ovoid seeds, 8-9 mm long, which are often borne singly in capsules. The precise affinities of *B. menziesii* need to be established. Other species of *Breweria*, however, have smaller seeds. *Breweria madrexa* of Australia has seeds 2 mm long, with two or more per capsule. *Breweria cordata* (= *Bonamia semidiis*) of Indonesia has four seeds per capsule, each 5-6 mm long. The fleshy outer testa of seeds of *B. menziesii* suggests attractiveness to birds, a feature which may or may not have been present in ancestral stocks. The fleshy outer testa is said to be mucilaginous, but is probably not sufficiently so to permit adhesion to bird feathers. Seeds of *Breweria* do not float.

**Ebenaceae:** The two Hawaiian species of *Diospyros* differ appreciably in fruit and seed size. The smaller-fruited species, *D. ferrea*, has fruits ca 18 mm long. These fruits are elongate, and thus much smaller in volume than those of the other Hawaiian species, *D. hillebrandii*. Fruits of *D. hillebrandii* are 20-25 mm long, 15-18 mm wide. Size of seeds parallels that of fruits. A typical seed of *D. ferrea* is 13 X 7 X 4 mm, whereas in *D. hillebrandii*, a comparable seed is 17 X 10 X 6 mm, approximately twice as great as that of *D. ferra* in volume. Appropriately, *D. hillebrandii* is much more restricted in distribution and ecology, occurring at about 2,000 feet in certain valleys on Oahu, whereas *D. ferrea* occurs at lower elevations, even down to near sea level, on all of the major islands. The fruit and seed size of other Pacific species of *Diospyros*, such as "Maba elliptica" and "M. savaiiensis" of Samoa is slightly smaller than that of *D. ferra* (Christophersen 1935). Evolutionary increase in size of fruits and seeds may be suspected in *D. samoensis* (non *Maba samoensis* Hieron.), the fruits of which are 45-50 mm long, with seeds about 30 X 9 X 5 mm.

**Elaeocarpaceae:** The Hawaiian species of *Elaeocarpus, E. bifidus*, has fruits which are ovoid, 22-30 mm long, 18-20 mm wide. This size seems best regarded, in view of the trends demonstrated in this paper, as an increase over fruit size in ancestral species. Large-fruited species of *Elaeocarpus* also occur on Samoa—4 cm long in *E. magnifolius*; 5 cm long in *E. ulianus* (Christophersen 1935). Fruit gigantism may characterize a number of genera in the Samoan flora, however. Species with much smaller drupes are scattered throughout the Pacific. *Elaeocarpus rarotangensis* of Rarotonga possesses drupes 12 mm in length (Brown 1935). *Elaeocarpus hookerianus* of New Zealand has drupes 8 mm long, and several Australian species have fruits in this range. Smaller-fruited species such as these may be suspected of being ancestral to the Hawaiian *E. bifidus*. Frugivorous birds are probably the agent of dispersal; fruits of *Elaeocarpus* lack floatability in water.

**Euphorbiaceae:** The native Hawaiian species of *Euphorbia* belong to sect. *Anisophyllum* (or, according to some authors, *Chamaesyce*) and range from seacoast to wet rain forest. Seacoast species, such as *E. degeneri* and *E. skottsbergii*, suggest
in morphology relationship to species of southeastern Polynesia: E. atoto, E. taitensis, and E. piteairnensis. Such coastal species as these may disperse by means of oceanic drift. Guppy (1906) lists seeds of E. atoto as floatable by virtue of air space within the seed coat. Mid-altitude Hawaiian species of Euphorbia may represent a different introduction; they are clearly different in their basic dispersal mechanism—which may be the same as that by which their ancestors arrived on the islands. Seeds of the low-altitude (but inland) species E. celastroides (Fig. 2) are small (1.5 × 1 × 1 mm), and are ridged and covered (when wet) by a prominent gelatinous coating. This suggests adhesion to birds' feathers as a means of dispersal. Species of high, wet forests, however, show marked fruit and seed gigantism. In E. clusiaefolia (Fig. 2), capsules range from 6–9 mm in length, and seeds are 3 mm in diameter. Not only are these seeds smooth, rather than markedly ridged or pitted, but also no appreciable gelatinous coating can be observed on them. This would seem clearly an instance of loss of dispersibility. Seeds of neither E. celastroides nor E. clusiaefolia float, and there is no reason to believe that their ancestors had floatable seeds. The Hawaiian species of Euphorbia which possesses the largest capsules is E. rockii, in which fruits measure 13–22 mm in length. Because capsules are so much larger than those of E. clusiaefolia, one would expect larger seeds in E. rockii. Unfortunately, study of all available specimens has revealed no capsules which contained anything but markedly shrunken seeds which are clearly infertile. These seeds are, as stated by Sherff (1938), 3–3.5 mm in diameter. One can only guess that well-formed seeds are somewhat larger than this, and information on this point would be very desirable. In any case, the large-seeded species of Euphorbia, which are restricted to upland wet forest areas, may be said to have clearly diminished dispersibility.

Goodeniaceae: The Hawaiian species of Scaevola represent three main groups: (1) S. sericea, which is widespread on beaches throughout the Pacific; (2) species such as S. gaudichaudiana and S. mollis with small purple ovoid drupes which are representatives of a montane group of species which extends from Australia to the Hawaiian Islands; and (3) S. glabra, a curious and isolated species of high wet forests on Oahu and Kauai, which has sometimes been treated under a segregate genus, Camphusia. Among the second group of species, some variation in size of drupe and endocarp does occur, but drupes mostly range from 4–10 mm in length, with the woody endocarp 3–7 mm long. Well outside this range of size is the fruit of S. glabra, which is speroideal or pyriform, 15–20 mm long. The endocarp is typically ovoid, ca 13 × 8 mm. The fruit dimensions of S. glabra clearly exceed those of any other Scaevolas of montane Pacific islands. Scaevola glabra probably represents an early immigrant to the islands, a hypothesis suggested both by its curious morphology and its restriction to relatively older mountains. If so, the greater time available for its evolutionary change on the Hawaiian Islands may have permitted it to approximate more nearly the large-fruited habit characteristic of trees of wet forest.

Halorhagidaceae: The Hawaiian species of Gunnera cannot be said to be large-fruited in comparison to forest trees, but they do represent marked increase in fruit size over species of other Pacific islands. Using dried fruits as a comparison, those of G. maurusiensis are 3 mm in diameter, whereas those of G. macrophylla (New Guinea) are ca 1.5 mm in diameter and those of G. prorepens (New Zealand) ca 1.2 mm in diameter.

Labiatae: Phyllostegia is endemic to the main Hawaiian Islands except for P. variabilis on Laysan Island and P. tahitensis on Tahiti. Phyllostegia and an endemic Hawaiian genus, Stenogynne, have been placed together in the tribe Prasieae. This tribe is distinctive in possessing genera with fleshy drupelets rather than dry nutlets.
Phyllostegia and Stenogyne may be derived from such ancestors as the Indo-Malaysian Genphotostemma, which also possesses drupelets. Because of the fruit morphology, dispersal by frugivorous birds may be suspected. Among the 24 species of Phyllostegia recognized by Sherff (1935), there is variation in size of the drupelets, but data are difficult to obtain because mature drupelets are unknown in some species, and although the size of dry endocarp of drupelets is known for the remainder, the dimensions of fresh fruits are rarely recorded. The average length of dried drupelets in Phyllostegia appears to be 2 mm, with fresh drupelets ca 4 mm long. The closely related genus Stenogyne (Fig. 3) shows a more dramatic series in increase of drupelet size. Species belonging to the section Microphyllae of Sherff (1935), such as S. diffusus, have small drupelets. Dried drupelets of these species are ca 2-4 mm long. These species inhabit dry, grassy areas on recent volcanic craters, such as Haleakala, Mauna Kea, and Mauna Loa. Most species, such as S. calaminthoides (Fig. 3), have drupelets which are 3-5 mm long when dried. A few species—usually those of very wet forest areas—have drupelets 6-8 mm long. These species grow in patches of forest adjacent to the high wet bogs of the Hawaiian Islands: S. kaalae (Mt. Kaala, Oahu), S. kamehamehae (Puu Kolekole, Molokai), and S. purpurea (Alakai Swamp, Kauai). The large-fruited Stenogyne shown in Fig. 3 was collected by the writer in Alakai Swamp and is presumably referable to S. purpurea, although it differs in leaf shape and in the size of the drupelets, which are appreciably larger than indicated by Sherff (1935). The series of fruit sizes in Stenogyne seems closely correlated with ecology and may perhaps be explained by the concept of precinctiveness. Increase in fruit size is accompanied in some species by a tendency to bear fewer drupelets per flower. Also, some species of Stenogyne (e.g., S. rotundifolia) have a tendency to envelop drupelets within a persistent tubular calyx which may hinder shedding of fruits.

The Hawaiian genus Haplostachys differs from the above genera in its dry nutlets. Although Fosberg (1948) suggests a common origin of this genus with Stenogyne and Phyllostegia, it may not be closely related. Most species of Haplostachys, such as H. linearifolia (Fig. 3), occupy dry grassy areas only a few feet above sealevel. Haplostachys munroi (Fig. 3), with larger fruits, grows in dry forest areas on Lanai. Fruiting calyces and also individual nutlets of all species of Haplostachys tested are capable of flotation in water, a fact which not only is suggested in the coastal habitat of the species, but which also suggests derivation of the genus independently of Phyllostachys and Stenogyne. The corky nature of the nutlet exocarp is responsible for floatability of the fruits. The larger seed size in H. munroi seems related to the

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**Fig. 3.** Fruits of the Hawaiian endemic genera Stenogyne and Haplostachys (Labiatae). Seeds of Stenogyne (which possesses fleshy drupelets) are shown to the right in each species. Fruits are shown with the facing portion of the enclosing calyx removed (except for S. purpurea).
entry of that species into the forest habitat. Occasional fruits of *H. munroi* are composed not of four triquetrous nutlets, but two larger hemispherical ones. Nutlets of *H. munroi* are often somewhat misshapen, with irregular margins.

**Lauraceae:** *Cryptocarya* in the Hawaiian Islands is represented by two close species, *C. oahuensis* and *C. manii*. Both of these are unusual in the genus in their large fruit size. Drupes in these species are spheroidal, 30–35 mm in diameter when dry; the figure 16 mm given by Rock (1913) is probably in error, perhaps based in immature material. These fruits are covered by a thin fleshy exocarp which overlies a thick (2–4 mm) woody endocarp. These features are in contrast with those of other species of *Cryptocarya*, in which fruits are much smaller and have a thin, almost papery endocarp which can be broken easily. In the Australian species *C. angulata* and *C. hyposporia*, fruits are ovoid, 11–12 mm × 8 mm when dry. Dried fruits of the Fijian *C. hornet* are somewhat larger, 16 × 14 mm. The presence of a fleshy, though thin, blackish exocarp suggests that frugivorous birds would be responsible for dispersal of these fruits. If so, the large size of fruits in the Hawaiian *Cryptocaryas* would seem to have foreclosed this avenue of dissemination. Large-fruited *Cryptocarya* are also present in Samoa: *C. samoensis* has drupes 40 × 17 mm, and *C. glaucescens* has similarly large fruits (Christophersen 1935). Dried fruits of *Cryptocarya* containing well-developed embryos are capable of flotation, but the fragile nature of endocarp in some species—as well as the fact that they are unlikely to be viable when thoroughly dried and washed out to sea—suggests oceanic drift as a relatively unlikely means of dispersal. *Cryptocaryas* are not lowland forest trees, which one would expect if they were seawater-dispersed. In the Hawaiian Islands, *Cryptocarya* occurs only in the geologically oldest areas (Kauai; Waianae Mts., Oahu), a fact which suggests that time has been available for evolution of the gigantic fruit size.

**Leguminosae:** Because native Hawaiian legumes are chiefly found in lower dry forest—down to the seacoast in many cases—and because legume seeds are notoriously capable of seawater transport without loss of viability (Guppy 1906; Ridley 1930), one might suspect that the Hawaiian legumes as a whole stem from such a history of immigration and have to various degrees evolved into forest habitats. Moreover, almost all genera represented in the Hawaiian indigenous flora contain non-Hawaiian species which are widespread beach species, known to be capable of seawater-flotation. Loss of floatability within the Hawaiian legumes would represent a discontinuation of this means of dispersal. Genera within the Hawaiian flora do have seeds which are black and shiny or colorful, suggesting attractiveness to seed-eating birds. Pods in the Hawaiian legumes mostly open poorly, however. Moreover, the large size of seeds in these species—like that in related non-Hawaiian species—suggests that such seed-eating birds would have to be large. Large seed-eating birds, such as parrots, have probably not played any appreciable role in long-distance dispersal, and dissemination of legumes to the Hawaiian Islands by oceanic drift seems the best hypothesis.

Seeds of the endemic *Erythrina sandwicensis* (Fig. 4) will not float, however. Seeds of other species of *Erythrina* do float. This fact was known to Guppy (1906), who reported floatability of seeds in *E. indica* and *E. ovalifolia*, failure of flotation in *E. sandwicensis* (then regarded as conspecific with the Tahitian *E. monosperma*). I have found that seeds of *E. variegata* (Fig. 4) also float. Moreover, the legumes in *E. variegata* remain closed and are themselves a flotation mechanism. Guppy (1906) attributed floatability of *Erythrina* seeds to a “light kernel”, since the tests does not float and mature seeds contain no air space. The difference in specific gravity be-
tween floatable *Erythrina* seeds and those of *E. sandwicensis* was investigated by means of hand sections on living seeds. My sections (Fig. 4) show that a prominent air-space system in cotyledons of *E. variegata* is probably responsible for flotation; airspaces are much smaller in cotyledons of *E. sandwicensis*. Legumes of *E. sandwicensis* could serve for seawater dispersal if they remained closed, but in fact, they do not. The only probable agent for dispersal might be the seed-eating honeycreeper *Psitacirostra*; if so, a shift in dispersal mechanism might be hypothesized. There seems little doubt that ancestors of *E. sandwicensis* arrived on the Hawaiian Islands by means of oceanic drift. The near identity of *E. sandwicensis* with the Tahitian *E. monosperma* and the tendency of both to occupy coastal stations, stations which are remote from those of other *Erythrina* species, would tend to support this idea.

A similar situation obtains with the Hawaiian kous (*Acacia koa* and *A. kauaensis*). Seeds of these will not float, and unopened mature pods will float only for a day or two. Dried branches bearing unopened but mature pods might be washed down to sea during torrential storms, and such "rafting" might be envisioned as a means of dispersal for this species. *Acacia koa* is very similar to *A. heterophylla* of Mauritius Island (Indian Ocean); the distance between the stations for these species alone suggests the likelihood of seawater dispersal. A phyllodial acacia which is similar to, but perhaps not immediately related to *A. koa* occurs on Samoa and Tonga: *A. simplicifolia*. The legumes of this species, unlike those of *A. koa*, do not open readily at all, and because each seed is sealed into a loment-like segment which contains an air space sufficient to float an enclosed seed, flotation would seem likely. Seeds of *A. simplicifolia* will not float when removed from the legume. The legumes, or segments thereof, will float for several days, but eventually become wetted and sink. *Acacia simplicifolia* is a beach species, and like the Hawaiian acacias, doubtless owes its arrival in Polynesia to oceanic drift. Probably Polynesian acacias came from a source in or near Australia, where phyllodial acacias are abundant. Pods of *A. koa* seem to show vestiges of adhesion between the two halves of the legume in zones which separate adjacent seeds, suggesting the *A. simplicifolia* condition. The fact that most pods of *A. koa* open readily means that the species is now ill-suited for seawater-dispersal (assuming that seeds remain viable at all when exposed to salt water). Koa may have been aided in their distribution throughout the major Hawaiian Islands by *Psitacirostra*, which was known to have sought these seeds.

The endemic Hawaiian *Sophora*, *S. chrysophylla*, forms another parallel. Seeds of *S. chrysophylla* will not float, a fact noted by Guppy (1906) and confirmed by me.
Legumes of this species, however, do not open readily. They are, moreover, formed with narrow constrictions between some of the seeds, so that either the entire legume or parts of it can float. Guppy claims that the legume in this species is too delicate to provide good flotation. Nevertheless, *Sophora* undoubtedly owes its original advent in the Hawaiian Islands to oceanic drift. Both legumes and individual seeds of *Sophora tomentosa* and *S. tetrapetra* float well. Legumes in these species are more durable than those of *S. chrysophylla*. At least some species of *Sophora* are still littoral species, such as *S. tomentosa*. Loss of dispersibility in *S. chrysophylla* is shown not only in fragility of legumes and failure of seeds to float, but in the fact that the species is adapted to inland dry forest primarily and to the extent it has left the coastal areas, it could not disperse by seawater regardless of floatability (except for rafting of branches washed down in streams).

Sauer (1964) reports that seeds are non-buoyant in the following endemic Hawaiian species of *Canavalia*: *C. galeata*, *C. molokaiensis*, *C. hawaiiensis*, *C. kauaiensis*, and *C. pubescens*. I confirmed non-buoyancy for the latter three species. Sauer seems to believe that species such as these were derived from a wide-ranging ancestor with buoyant seeds, an interpretation my studies would endorse. Other Pacific species of *Canavalia* which are restricted to one island or several nearby islands and which have non-buoyant seeds include *C. vitiensis* (Fiji), *C. raiateensis* (Raiatea), and *C. megalantha* (Marianas Is.); wide-ranging species of the Pacific with buoyant seeds include *C. sericea* and *C. maritima* (Sauer 1964).

Seeds of the Hawaiian endemic *Mezoneurum kauaiensis* showed no floatability in my experiments. Mixed results were obtained with seeds of *Strongylodon lucidus*: of five seeds tested, only one floated. This suggests poor floatability at best. Seeds of *Mucuna gigantea* (a coastal element in the Hawaiian flora) did float.

The above results suggest that loss of buoyancy—and thereby dispersibility—has occurred quite conspicuously in Hawaiian Leguminosae. Loss of dispersibility in these seems to have occurred almost in direct proportion to the extent to which the species have adapted to upland forest conditions.

**Malvaceae:** The problem of whether or not the Hawaiian and Tahitian cottons are native has been discussed by Stephens (1963, 1964), who concludes that they are probably native and that a hypothesis of pre-historic natural arrival by means of oceanic drift seems most acceptable. To be sure, as Guppy (1906) and Stephens (1958) note, seeds of the Hawaiian *Gossypium sandvicense* (= *G. tomentosum*) sink within a day or two, as soon as their fibers become thoroughly wetted, and capsules float even more poorly. Nevertheless, seeds of most cottons retain great viability after soaking in seawater (Stephens 1958), and this fact, together with their preference for habitats along the immediate coast, strongly suggests oceanic drift as a means of dispersal. Attachment of seeds to birds by means of the fibers is not inconceivable, however. Seeds of the Galápagos cotton (*G. barbadense* var. *darwinii*) float for prolonged periods (Stephens 1958), indicating that in at least a portion of the genus this ability is present. In view of the considerations presented in this paper, loss of floatability in the Hawaiian cotton would not be surprising. The Hawaiian cotton has, in any case, been able to reach all the major islands of the group, and lack of subspecific variation (Stephens 1964) suggests that dispersal from island to island within the Hawaiian group may recur rather frequently. Whether or not entire plants with capsules attached can, when dry, float is a question which needs investigation.

The peculiar endemic Hawaiian genus of tree-cottons *Kokia* may be suspected of having been derived from a *Gossypium*-like ancestor. With *Kokia*, the problem is
much like that of *Gossypium*. *Kokia* species occupy arid lowland sites, characteristic of species introduced by oceanic drift. Seeds of *Kokia cookii* and *K. rockii* float for several days, but sink as soon as the fibers become thoroughly wetted. This degree of floatability might suffice for dispersal of the genus throughout the major Hawaiian Islands. Capsules in *Kokia* float only for a few hours. Capsules of *Kokia* ordinarily flare widely, releasing seeds, so seed flotation, as with *Gossypium*, seems a possible means of dispersal.

Precisely the same results as with *Kokia* were obtained with species of another Hawaiian genus, *Hibiscadelphus*. Tests were made on seeds and capsules of *H. giffordianus*, *H. hualalaiensis*, and *H. wilderianus*.

Of the endemic species of *Hibiscus* tested (*H. arnottianus*, *H. brackenridgei*, *H. immaculatus*, and *H. waimeae*), none possessed flotation ability either in seeds or capsules. If these species did stem from seawater-dispersed ancestors, this ability has been entirely lost. Seeds of the widespread littoral *Hibiscus* of the Pacific, *H. tiliaceus*, do float, and have undoubtedly dispersed in this fashion. In addition, tests on seeds of the non-insular *H. mutabilis* showed that seeds, even when deprived of their covering of hairs, float indefinitely. Dispersal of *Hibiscus* species, like *Gossypium* species, throughout the Pacific by means of oceanic drift might still logically be postulated. Dispersal of hispid seeds in bird feathers is another possibility which cannot be ignored. Seeds of a few of the native Hawaiian *Hibiscus* species still possess some stiff hairs. In either case, loss of dispersibility seems to have occurred in Hawaiian *Hibiscus* species, a loss correlated with evolution into moist upland sites.

**Nyctaginaceae:** The native Hawaiian Nyctaginaceae probably show relatively little loss of dispersibility with respect to fruit morphology. The fact that *Pisonia (Ceodes) umbellifera* is absent from some suitable islands in the Pacific might be due to the large size of fruiting perigones, although the perigones are markedly viscid. The same may apply to *Pisonia (Rockia) sandwicensis*, which is endemic to the Hawaiian Islands. This species was cited by the writer (1965) as an example of loss of dispersibility. The sticky perigones suggest retention of ability at dissemination by birds, but the ecological preference of this species—forests between 2,000 and 4,000 feet altitude—would place it well out of the range of seabirds, which would be the best means for long-distance dispersal. The loss of dispersibility in *P. sandwicensis* may be said to consist not of morphological change, but in ecological shift and attendant cessation of contact with long-range vectors.

**Pittosporaceae:** Fruiting structures which are exceptionally viscid can be quite large and still, presumably, retain good dispersibility. Increase in size of seeds in the Hawaiian species of *Pittosporum* may not, therefore, actually cancel their ability to be transported, although it would seem to diminish the probabilities somewhat. Species of *Pittosporum* with very large seeds have evolved in the Hawaiian Islands, and this seed gigantism may be primarily related to ecological adaptation to shady forests. Also, adaptation to high forests puts *Pittosporum* out of the range of seabirds. According to Rock (1913), however, the Hawaiian crow seems *Pittosporum* seeds. Such a bird may, during feeding, collect seeds on feathers and occasionally transport them to new localities within the Hawaiian Islands. Seeds in most of the Hawaiian species of *Pittosporum* recognized by Sherff (1942) are somewhat discoid in shape, from 5–7 mm long. Species with larger seeds (7–9.5 mm) include *P. sulcatum*, *P. dolosum*, *P. cauliiflorum*, and *P. hawaiiense*. Relatively smaller seed sizes characterize South Pacific species (longest dimensions given): *P. niueana* (4–5 mm), *P. toitense* (ca 4 mm: Fig. 5), *P. rarotongense* (4.5–5 mm), and *P. rapense* (5.5–6 mm). Seeds of Australian and New Zealand *Pittosporum* species are much smaller by comparison: many
of them have seeds no more than 3 mm long, as in *P. tenuifolium* (Fig. 5). Species in the western Pacific have relatively small seeds also: *P. megacarpum*, of the Philippines (4–6 mm); *P. resiniferum* of the Philippines (3–4 mm) and *P. moluccanum* of the Philippines and Indonesia (3 mm).

**Primulaceae**: Although some Hawaiian species of *Lysimachia* have large woody capsules (such as those of *L. forbesii*, which seem to open poorly), seeds are no longer than 2 mm, a size which suggests ease in dispersibility. Gigantism in fruits without corresponding increase in seed size also characterizes other Hawaiian genera: *Labordia*, of Loganiaceae, compared with the closely related South Pacific species of *Geniostoma*; *Cyanea* and *Clermontia* of the Lobeliaceae, compared among themselves.  

**Ranunculaceae**: The two endemic Hawaiian species of *Ranunculus*, *R. maviensis* and *R. hawaiianus*, differ from each other with respect to the degree to which achenes are beaked. Neither species has a stigmatic beak which is hooked. A *Ranunculus* with a hooked achene may not be ancestral to these species. The size of achenes in the Hawaiian ranunculi (2–4 mm) is not so large as to preclude the possibility of long-distance dispersal, although it is relatively large in comparison with many species of *Ranunculus*. Species with achenes similar in morphology and size to the Hawaiian species include *R. fibrosus* and *R. plebius* (Java) and *R. sieboldii* (Java).

**Rhamnaceae**: The Hawaiian *Alphitonia ponderosa* has, as noted by Hillebrand (1888), larger fruits (ca 13 mm in diameter) than *A. zizyphoides* of Tahiti and Tonga (ca 10 mm in diameter) or *A. franguloides* of Fiji. *Alphitonia marquisensis* of the Marquesas Islands has fruits nearly as large (12 mm in diameter). These are also good indications of seed size. *Alphitonia ponderosa* has seeds measuring $6 \times 5 \times 2$ mm, whereas those of *A. marquisensis* are $4 \times 3.5 \times 1.5$ mm and those of *A. zizyphoides* are $4.7 \times 3.5 \times 1.5$ mm. These distinctions, although they follow a trend toward larger seed size in the Hawaiian Islands, would not seem particularly important. However, one should note that in *A. zizyphoides* and other species, the fleshy exocarp and the woody cocci which the exocarp encloses fall from the mature fruit, leaving a pair of brownish seeds, surrounded by contrasting red arils, exposed upon the pedicel. This presentation would seemingly offer an excellent display for seed-eating birds. However, Hillebrand (1888) notes that in the Hawaiian *A. ponderosa*, the exocarp does not fall away so that seeds are not, in fact, exposed. To the extent to which this fruit dehiscence fails to occur, *A. ponderosa* can be said to have lost dispersibility.

Two species of *Colubrina* are native to the Hawaiian Islands. Of these, *C. asiatica* is wide-ranging in the Pacific and occurs near the seacoast on the many islands where it is found. *Colubrina oppositifolia*, on the other hand, is endemic to the Hawaiian.
Islands and occurs inland in the lower scrub forest. The two species differ in floatability of seeds, a fact noted by Guppy (1906) and confirmed by me. However, Guppy’s observation that seeds of *C. oppositifolia* would float for “a week or two” is probably based on faulty material. Specimens I tested had mature germinable seeds; these seeds sank immediately upon being dropped into water. Seeds of *C. asiatica* float indefinitely, as Guppy claims. Anatomically, tissues of the seeds in the two species appear similar. Ability of seeds of *C. asiatica* to float is probably due to a prominent space which forms between cotyledons and endosperm (Fig. 4). No such space was observed in my seeds of *C. oppositifolia* (Fig. 4). When the testa is removed from seeds of *C. asiatica* so that water can penetrate the air space, they sink. In addition, the seeds of *C. oppositifolia* are larger (6-7 × 5 × 3 mm) than those of *C. asiatica* (4 × 4 × 2.5 mm), as shown in Fig. 4. As noted by Hillebrand (1888), fruits of *C. oppositifolia* do not dehisce well: “. . . the epicarp woody and not separating from the endocarp, therefore the cocci separating tardily and imperfectly.” Seeds of *C. asiatica*, on the contrary, are readily released. *Colubrina oppositifolia* may be assumed to have originated from ancestors like *C. asiatica* which reached the Hawaiian Islands through oceanic drift. *Colubrina oppositifolia* seems a good example of both loss of dispersibility and increase in seed size. The latter characteristic may represent an adjustment to the forest habit, for *C. oppositifolia* is a tree, whereas *C. asiatica* can only be regarded as a shrub.

**Rosaceae**: The Hawaiian *Acaena*, *A. exigua*, appears closer in morphology to the Californian *A. californica* than to any of the *Acaenas* of the South Pacific. On New Guinea, New Zealand, and the Juan Fernández Islands are species of *Acaena* in which the fruit-enfolding calyx bears only a few long prongs, each tipped by a prominent crown of retrorse barbs. On both *A. californica* and *A. exigua*, however, the calyx is covered by a scattering of short prickles (Fig. 5). In *A. californica*, these prickles bear retrorse barbs. In *A. exigua*, the barbs are lacking. The small size of fruiting calyces in *A. exigua* suggests that it presents no problem for dispersal. However, loss of barbs may well have occurred following arrival on the Hawaiian Islands. If so, this would denote a loss of dispersal mechanism similar to the loss of retrorse barbs on Hawaiian species of *Bidens* (Carlquist 1966b).

Of the two endemic species of *Rubus* on the Hawaiian Islands, one, *R. macrocarpi*, is conspicuous because of its large fruits, 2–3 cm in diameter. The endocarp of each achene in this species measures ca 4 × 3 × 3 mm, a size which is appreciably larger than that of *R. hawaiiensis* (4 × 2 × 1 mm) or South Pacific species of *Rubus*, such as New Zealand’s *R. australis* (2.5 × 2.5 × 2 mm).

**Rubiaceae**: Fruits of most drupaceous Hawaiian Rubiaceae are 1 cm or less in diameter and thus may be considered still readily dispersible. Seeds in capsular Hawaiian Rubiaceae are relatively small, mostly 2 mm or less in length. Selected comparisons within these genera would probably show larger fruit and seed size within the species of wet forest, as well as greater overall size of fruits and seeds in Hawaiian species as compared to relatives from continental areas of the western Pacific. For example, *Timonius polygamyus* from Rimitara (Austral Is.) has drupes ca 8 mm in diameter. The seeds are about 2.5 × 2.5 × 1 mm. In *Bobea elatior*, representative of an endemic Hawaiian genus closely related to *Timonius*, drupes are slightly larger (10 mm in diameter) with fewer and larger (6 × 3 × 1.5 mm) seeds. Among non-Hawaiian Polynesian Rubiaceae, the Samoan genus *Sarcopyge* contains an interesting series of increasing fruit and seed size.

**Rutaceae**: Hawaiian Rutaceae belong to three genera: *Pelea, Fagara*, and *Platydesma*. *Pelea* is endemic to the Hawaiian Islands and the Marquesas and is proba-
bly most closely related to *Evodia* of the South Pacific, although *Melicope* and *Acronychia* of that region also show many resemblances. *Platydesma*, an endemic Hawaiian genus, seems to have evolved from a *Pelea*-like stock. *Fagara* (*Zanthoxylo-

lum*) is well represented in the Old World tropics. All three genera represented in the Hawaiian Islands have follicular fruits which open at maturity, revealing shiny black seeds which, though not fleshy, are doubtless attractive to birds. Within each of these genera, a trend toward gigantism of fruits and seeds is evident.

*Pelea* shows a notably wide range of fruit and seed sizes. The three species figured in Fig. 6 suggest some extremes and an intermediate size for the genus. *Pelea waialalae*, with very small seeds, might at first glance seem, if the principles suggested in this paper are correct, like a lowland species, instead of (as it is) a native of high open bogs. Actually, the correlation of small seed size with the open bog habitat is understandable, because smaller seeds seemingly characterize the bog plants of the Hawaiian Islands, whereas seeds of forest plants are much larger. This suggests that one factor which has been operative in increase of fruit and seed size in *Pelea* is adaptation to the large-seeded forest-tree habit; preciinctiveness may also play a role. A feature which appears to accompany increase in fruit size in *Pelea* is the tendency for seeds not to be exserted, as they are in *Evodia samoensis* (Fig. 6). In *Pelea*, the funiculus which in *Evodia* aids in display of seeds is present, but does not have that function. Mature fruits in *Pelea* exhibit loculicidal dehiscence of follicles, followed by shattering of the valves and fall of seeds.

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**Fig. 6.** Comparison of fruits and seeds of Hawaiian and non-Hawaiian Rutaceae. The genus *Pelea*, endemic to the Hawaiian Islands and the Marquesas, is closely related to *Evodia*, one species of which is shown for comparison. For each species of *Evodia* and *Pelea*, a view toward the summit of the fruit and a view of a longitudinal section of a fruit are shown. There are mostly two seeds per follicle in *Pelea*; because follicles are shown sectioned, only a single seed is visible. Habit of fruits and seeds are shown for two Hawaiian and one non-Hawaiian species of *Fagara*. One or two follicles may develop in the Hawaiian species. Two species of the endemic Hawaiian genus *Platydesma*, which may be closely related to *Pelea*, are shown. Scale applies to all drawings.
In the genus *Fagara*, a wide range of fruit and seed sizes is visible, as suggested in Fig. 6. The seed size shown for *F. oahuensis* may be said to represent a minimal size for Hawaiian Fagaras, as well as one which characterizes all Hawaiian species except *F. dipetala*. This same size can be found in seeds of *F. pinnata* (Tonga), *F. megistophylla* (Fiji), and *F. gillespieana* (Fiji). The seed size in the Hawaiian *F. dipetala* (20 × 14 × 12 mm) is remarkable, however, and represents a definitive diminution of dispersibility. Contrastingly minute fruits and seeds are shown for the Japanese species *F. ailanthoides* (Fig. 6).

Within the genus *Platydesma*, a marked increase in fruit and seed size may be seen by comparing the species *P. cornuta* and *P. remyi* (Fig. 6). A feature in *Platydesma* which is of interest in connection with loss of dispersibility is Rock’s (1913) observation regarding *P. campanulatum* (= *P. spathulatum*): “The capsule often rots away but the seeds remain attached to the placenta for some time.”

**Santalaceae**: The Hawaiian species of *Santalum* form a good series with respect to size of drupes. At maturity, drupes in *Santalum* are reddish or purplish in color. The majority of the Hawaiian sandalwoods have drupes from 8–12 mm in diameter, a size which, together with the nature of the fruit, makes dispersal by frugivorous birds likely. Species of *Santalum* elsewhere, such as *S. album*, also have drupes in this size range. Rather small drupes occur in *S. ellipticum* var. *littorale* (6–7 mm long) and *S. cuneatum* (8 mm in diameter); both of these are lowland Hawaiian plants, growing on the coastal plain. Notably large-fruited is *S. pyrularium*—characteristic of dry but upland forests of Kauai. In *S. pyrularium*, drupes attain 25 mm in length, and are ca 15 mm in width. The endocarp measures about 15 × 10 × 10 mm. This large size suggests dispersal by birds would no longer be very effective.

**Sapindaceae**: Of all examples of gigantism in fruits in the Hawaiian flora, none is perhaps so dramatic as that of *Alectryon*. This genus of about 30 species ranges from Australia, New Zealand, New Guinea and the Philippines through Melanesia; in Polynesia, it is represented in Samoa and the Hawaiian Islands. Most species have relatively small fruits, as represented in Fig. 7 by *A. carinatus* and *A. excelsus*. Cocci of *A. carinatus* measure 10 mm in diameter if borne singly; if borne in pairs, each coccus is ca 8 mm long, 6 mm wide. In *A. excelsus*, single cocci are 12 mm in diameter, paired cocci 10 mm each. As the drawings for various species of *Alectryon* show, mature cocci open somewhat irregularly, exposing the expanding fleshy reddish aril at the tip of which the seed is borne. The relatively small size of the seed in *A. carinatus*, *A. excelsus*, and other small-fruited Alectryons, together with the contrast between reddish aril and blackish or brownish seed, suggests ease in distribution by frugivorous birds. The seeds in the two above-mentioned species are only 5–6 mm in diameter, and would be easily swallowed by a bird seeking the arils. If so, the remainder of the species shown in Fig. 7 may be said to form a series in loss of dispersibility. *Alectryon grandifolius* of Fiji has single cocci 22 mm in diameter, paired cocci 18 mm each. The seed measures about 12 × 10 × 8 mm, and thus by itself would be as large as the smallest drupe (including fleshy exocarp) one would expect birds ordinarily to have carried over long distances. *Alectryon samoensis* is well beyond this range. Single cocci measure ca 35 mm in diameter, and paired cocci about 30 × 28 mm each. The seeds are about 22 × 20 × 20 mm. The Hawaiian species of *Alectryon* represent the logical conclusion of this trend toward gigantism. *Alectryon macrococcus* and a closely related segregate species, *A. mahoe*, have fruits somewhat variable in size but of enormous proportions. In these species, cocci borne singly may reach 60 mm in diameter. When borne in pairs, each coccus is ca 34 × 40 mm. Seeds in these species can easily be 32 × 30 × 20 mm. Dispersal of such seeds by frugivorous birds—especially those native to the Hawaiian Islands—is unthinkable. Seeds
Fig. 7. Comparison of fruits and seeds of non-Hawaiian species of Alectryon (Sapindaceae) with those of the Hawaiian A. macrococcus. One or both cocci of the fruits may develop in all species. At maturity cocci are broken open by the expanding reddish aril, at the tip of which the seed is borne. For each species, an opened monococcate and an unopened bicoccate fruit are shown; also two views of a seed: one lateral (chalazal end of seed above) and one polar (surface opposite chalazal end shown). Dotted lines around lateral views of seeds of A. samoensis and A. macrococcus indicate outline of aril. Scale applies to all drawings.

of this size would tend to drop within a short range of the parent plant, so that a high degree of precinctiveness seems likely. Tendency to reproduce within the moderately dry mid-altitude forests where this tree is native may explain the gigantism. The value of a large amount of storage tissue within seeds does not seem preeminent in the relatively open forests where this species lives, although it may be a factor. One can postulate that the immigrant ancestors of the Hawaiian Alectryons had fruit and seed sizes comparable to those of A. excelsus. Gigantism of fruits in the Samoan Alectryon has probably been achieved parallel to that of the Hawaiian species, and follows a trend toward fruit and seed gigantism in the Samoan flora.

Sapindus oahuensis is also notable for relatively large fruits and seeds. In this species, only one of the two potential drupelets per flower ordinarily matures. Each drupelet when fresh measures ca 33 X 24 X 20 mm. The seed measures ca 21 X 12 X 10 mm. The fleshy exocarp, which has a date-like odor and texture when drying, suggests that the ancestors of S. oahuensis were sought by frugivorous birds. To be sure, there are species with large fruits elsewhere in the Pacific, such as S. mukorossi, which occurs in the Bonin Islands. The wide-ranging Sapindus saponaria, however, has fruits 15–18 mm in diameter, with seeds mostly less than 10 mm in length. Such a species—or one with even smaller fruits—seems likely to have been ancestral to S. oahuensis. Neither fruits nor seeds of Sapindus are capable of flotation.

Sapotaceae: The Hawaiian genus Planchnolla (Sideroxylon of earlier authors) is represented in the Hawaiian Islands by a single highly polymorphic species, P. sandwicensis. Segregate species were recognized by Rock (1913). There are distinctive populations within P. sandwicensis, some notable for distinctive fruit shapes
and sizes. Some fruits of *P. sandwichensis* are only 2 cm in diameter at maturity, with seeds about $17 \times 6 \times 3$ mm. Others, as in the population recognized by Rock as *S. rhynchospermum*, are 5.5 cm in length, 3.5 cm or more in diameter, and contain seeds $35 \times 14 \times 3$ mm. Thus, within the Hawaiian Planchonellas there may be said to be tendencies toward fruit and seed gigantism. The smaller fruit and seed size mentioned above is about the same as those of species of *Planchonella* on other Pacific islands, such as *P. costata* = *vitiensis* of Fiji, *P. garberi* of Samoa, and *P. novozelandica* of New Zealand. The size of fruits in these species seems excessive for over-water dispersal by frugivorous birds. Although fruits can be viscid, the seeds are exceptionally smooth and would not adhere easily to birds. However, tests on flotation prove that dried fruits of *Planchonella* float almost indefinitely, perhaps because the papery endocarp with which each seed is surrounded contains a generous air space around each seed. Individual seeds also will float, at least for several days. Because *Planchonella* is a component of lowland forests, often along the immediate coast, one might suspect that at least some species are distributed by oceanic drift. Also, the fact that the same subspecies (according to Karin's determination) which occurs on Fiji is also present on Rurutu in the Austral Islands is suggestive of oceanic drift. A species which is frequently re-introduced by seawater flotation would not be expected to give rise to endemic species on an island.

**MONOCOTYLEDONS**

**Liliaceae:** Exact systematic affinities are difficult to establish for the Hawaiian Dracaenas, of which two species, *Pleomele aurea* and *P. fernaldii*, have been recognized. This endemic genus is a segregate of *Dracaena*, and some authors prefer to retain the Hawaiian species under *Dracaena*. With regard to species of *Dracaena* elsewhere in the world, one may say that in most species fruits are 5–9 mm in diameter, and contain several seeds each 3–5 mm long. Such fruits might have been ancestral to the Hawaiian Dracaenas. Such fruits would be edible by birds. Fruits of Dracaenas are not known to float. *Pleomele fernaldii* has fruits 10–12 mm long, 5–10 mm in diameter if one carpel develops, 10–17 mm in diameter if two or three carpels develop. Seeds are about 4–8 mm in diameter. In *P. aurea*, fruit and seed size vary somewhat, but fruits are usually 14–25 mm in diameter, with seeds 9–18 mm in diameter when fresh. *Pleomele aurea* is a tree which ranges from dry lowland lava areas to well into higher portions of dry (*Acacia–Metrosideros*) forest. Relatively large fruits can be seen on trees in the latter region. *Pleomele* may be said to exhibit marked gigantism of fruits and seeds.

**Palmae:** *Pritchardia* is a palm which ranges from Fiji to the Hawaiian Islands and which may be regarded as an extension of *Livistona* of Asia and Indo-Malaysia. The westernmost species, *P. pacifica* and *P. thurstonii* of Fiji, have the smallest fruits, 12 and 7 mm in diameter, respectively. The Hawaiian Pritchardias have been split into a large number of species by Beccari and Rock (1921); only a fraction of these seem likely to be recognized by most workers. The polymorphic nature of *Pritchardia* in the Hawaiian Islands is evident, however. Most of the Hawaiian species recognized by Beccari and Rock have fruits which vary from 20–30 cm in diameter. Ten of the species they recognize have fruits which exceed 40 cm in diameter. Of these, some have quite gigantic fruits (6 × 4 cm in *P. lowreyana*; 5 × 3 cm in *P. rockii*; 5.5 × 4 cm in *P. montis-kea*). Beccari and Rock (1921) note the irony in the fact that large-fruited species such as these tend to occur in pockets high in wet rain forest, situations to which access by such cumbersome fruits seems unlikely. Dried fruits, however, have a relatively low specific gravity and might be transported short
distances by violent winds. To explain the development of such large fruits in Hawaiian Pritchardias, Beccari and Rock invoke the concept of precinctiveness, which seems quite acceptable. Regarding the possible mode of introduction of *Pritchardia* to the Hawaiian Islands, one could say that the relatively small size of fruits in the Fijian *P. thurstonii* would suggest edibility and therefore transport by frugivorous birds. However, there is a distinct possibility of oceanic drift also. My tests of fruits of *P. martii* (summit of Castle Trail, Oahu) showed that fresh fruits sink immediately when placed in water. However, these same fruits, if allowed to dry for several days and then placed in water, were capable of floating indefinitely (in my tests, two weeks, at which time the experiment was terminated). The occurrence of *Pritchardia* on such a low and dry island as Nihoa, in the Hawaiian Leeward chain, as well as on low small islands in southeastern Polynesia, suggests the possibility of seawater dispersal, at least on rare occasions. The Nihoa species, *P. remota*, is relatively small-fruited (18–20 × 17–19 mm). The large-fruited species from the major Hawaiian Islands can all be said to be characteristic of wet rain forest. Thus, the correlation between fruit size and ecology can be said to exist in *Pritchardia*.

**DISCUSSION AND SUMMARY**

The hypothesis presented in this paper depends upon the strongly disharmonic nature of the Hawaiian flora. Because the number of immigrants to the Hawaiian Islands was relatively small, and because these immigrants were confronted with relatively large land area, suitable climate, diverse topography, and geographical isolation, they have undergone a great deal of evolutionary change—particularly with regard to gross morphology. One aspect of this change is loss in dispersal ability. In a continental situation, evolutionary change for any particular group is hindered by the presence of so many resident groups, and changes in habit and ecological preference are limited in all such groups, at least over relatively short periods of time. Just such short periods of time, on the other hand, have probably been able to foster dramatic evolutionary changes on oceanic islands.

The dispersal mechanisms and ecological preferences which permit transport to and establishment upon oceanic islands tend to be those of "weedy" species: capacity for dissemination across long distances, ability to grow in open, often dry, habitats. On a continental area, ecological preference and dispersal ability show a much wider gamut: from open habitats to stable wet forests, from good dispersibility to virtually nil. Hence the evolutionary curriculum of immigrants to oceanic islands may feature re-creation of a continental spectrum of adaptations from the limited fund of waifs which the island receives. Gigantism in size of fruits and seeds in the Hawaiian Islands can, in part, be explained on the basis of such re-creation of the large-seeded habit characteristic of forest trees. This habit is supposedly related to the greater volume of stored food materials required for success of a seedling under shady forest conditions.

Another aspect of this phenomenon is that of precinctiveness, or tendency to distribute propagules within a limited distance of the parent plant. In a stable forest situation, one would expect natural selection to favor this tendency, for excellent dispersibility would carry large numbers of propagules to open, arid, or otherwise unsuitable habitats—even out to sea. The number of propagules produced and their dispersibility may be expected to conform to a level sufficient to maintain a species in a suitable area. Exceptionally high or low rates would be unfavorable. Relatively low rates of reproduction and dispersal would be favored in Hawaiian forests, which
are very limited in geographical extent—as are the islands themselves. A single
mountain, valley, or ridge may represent the area to which a species is adapted.
Moreover, the number of species occupying a given forest area in the Hawaiian
Islands is moderate, so a relatively poor rate of reproduction and dispersal will suf­
fice to maintain such a species. In a comparable continental forest area, the number
of species is much higher, the probable attrition of propagules of each species high.
so despite adaptation to the forest habitat, a continental species might be expected
to maintain a higher rate of reproduction and dispersal. This would tend to explain
why a number of genera represented both in forests of continents or continental
islands and the Hawaiian Islands tend to reach maximum fruit and seed size in the
Hawaiian Islands (Aelectryon, Fagara, Tetraplasandra, etc.). It would also tend to
explain why little such gigantism can be observed west of the andesite line in the
Pacific, where genera also in the Hawaiian flora are concerned.

Returning to the nature of immigrants to oceanic islands, one can say that many
of them, during evolution on islands, are destined to lose contact with the vector
which originally brought them to the islands. To the extent to which this is true,
the dispersal mechanism related to that vector will lose selective value, and the
mechanism will be lost or a new mechanism and vector substituted. This seems easily
demonstrable in the case of seawater-dispersed species. As long as such a species re­
tains (a) dispersibility only by oceanic drift; and (b) ecological preference for litt­orsal sites, it will remain in coastal locations. Its entry into upland habitats may be
facilitated if it can cease dispersal via seawater and thus become isolated, for littoral
populations would tend to swamp out an ecological shift. Although some species
excel at oceanic drift, others (such as Acacia and Gossypium) may be only occasion­
ally successful in this regard. If an Acacia establishes with great rarity on an island,
populations may be able to shift into upland sites before a second introduction of the
species reinforces the littoral preference. Schimper, in a letter quoted by Guppy
(1906), failed to see why seawater-dispersed plants would benefit from loss of float­
ability; the above reasons appear quite compelling to me. Guppy appears to have
misunderstood this problem by assuming that oceanic drift is an all-or-nothing-at-all
phenomenon. He fails to take into account the possibility of rare introductions, and
thus his list of native Hawaiian plants derived from seawater-dispersed ancestors is
much smaller than mine (see Introduction). In particular, Guppy neglects the poss­
sibility that seeds poor at flotation yet resistant to salt water (e.g., Gossypium) may
have arrived via rafting.

Similar considerations would apply to species to which other types of vectors are
ancestral. One can imagine that a dispersal mechanism—particularly when it is in
the form of an appendage (i.e., the awns in Bidens)—might vanish because it att­
tains a neutral selective value. Such an appendage, if related to transport by marine
birds, will lose value if the species evolves into forests where marine birds are absent.
Loss of the appendage, in fact, might “release” the plant from a close association
with seabirds and permit the ecological shift. Long-distance dispersal to an island is
a rather drastic event, and subsequent dispersal within an island is likely to be dif­
ferent. To the extent that it is different, the dispersal mechanism may change. One
can imagine that, for example, frugivorous birds which bring a plant to an island may
not themselves establish there.

A notable feature seen in several Hawaiian genera with seed gigantism is the
tendency to produce fewer seeds as well (Stenogyne, Breweria, Fagara, Plantago
princeps). Another interesting tendency, perhaps the by-product of gigantism, is the
production of odd-shaped seeds (Dianella, Haplostachys, Stenogyne, Alsinodendron,
Pittosporum). This tendency was also noted in insular Compositae with fruit gigan­
tism, such as Dendroseris (Carlquist 1966b).
Especially important with regard to loss of dispersibility is the fact that some features are either not visible in terms of morphology or are difficult to demonstrate. Relative ability to disperse can only be suspected, because one almost never sees an event of dispersal from release of a seed to actual successful establishment. One cannot easily demonstrate how narrow the zone of ecological adaptation may be for a particular species. One can suspect that many Hawaiian species or phylads began as rather weedy groups, but have now lost this pioneering ability in favor of specialized preferences (e.g., wet forest). The fact that narrowly endemic Hawaiian species, particularly in geologically old and moist forest regions, are also the ones which best show loss of dispersibility (e.g., *Tetraplasandra waimeae*; *T. waialaealae*; *Scaevola glabra*) should come as no surprise. Many other Hawaiian species, such as a number of *Lobeliaceae*, may show specialized ecological preference without visible loss of dispersibility, however.

Another source of loss of dispersibility is also difficult to demonstrate: short seed viability. This, too, would be expected to characterize species of moist forest areas. One must not assume that the contemporary seed viability of a species is the same as that of its ancestors. The ecological shift from dry forest to wet forest would be expected, in fact, to be accompanied by marked shortening of seed viability. Loss of ability to resist salt water (in species which immigrated via seawater) and loss of ability of seeds to survive digestion by birds (in groups brought by frugivorous birds) would also constitute cryptic losses of dispersibility. The importance of elusive factors such as these, even though they are not studied in the present paper, cannot be too strongly emphasized.

The data in the main section of this paper suggest that loss of dispersibility is greatest in plants of high, wet forests. For angiosperm groups which range from coast to mid-elevations, the upper altitudinal ranges seem to have favored this phenomenon most. Relatively little loss of dispersibility seems to have occurred in species of the high Hawaiian bogs. Bog species may be mostly incapable of ecological shift into forests, and bogs may, in a sense, represent open or pioneering habitats. The primary adaptation of the majority of immigrants to the Hawaiian Islands appears to have been dry upland forest. The dry upland forest is still the center for the greatest diversification and richness in speciation (Rock 1913). These circumstances appear logical in view of (1) tendency for immigrants to be plants of pioneering habitats; (2) relative abundance in area and accessibility (to birds, etc.) of dry-forest areas in the Pacific as source and recipient areas; (3) specializations of wet-forest species, such as short viability, which renders them poor as immigrants. Such considerations have been endorsed by Wilson (1959) in his studies of Pacific ants. The wet forests of the Hawaiian Islands, therefore, may be thought of as a secondary formation, populated by species which have, in many cases, migrated from upland dry forest.

Although the Hawaiian forest flora shows marked loss of dispersibility, examples can be found elsewhere in Polynesia (Carlquist 1966b). Examples in the present paper suggest that the phenomenon is well represented in Samoa (*Alectryon*, *Cryptocarya*, *Diospyros*, *Elaeocarpus*, *Sarcopyge*).

No real cases in which dispersal ability has improved autochthonously in the Hawaiian flora seem to exist. The peculiar shaker-mechanism and winged seeds of *Trematolobelia* (Carlquist 1962) suggest solution of problems of dispersal in areas of very high rainfall. The pseudobaccate fruiting calyces of *Alsinodendron* are an interesting shift in mechanism, perhaps for similar reasons; flowers of *Alsinodendron* are pendant, and thus flowers and capsules are not exposed to direct rain.

For various reasons, precise statistical expressions of loss of dispersibility have not been undertaken here. Nevertheless, the examples described above, together with those presented earlier, show clearly the reality of this phenomenon. Emphasis should
be placed on the fact that dispersal mechanisms, like other features of a plant related to ecology, are constantly changing, and that there is no reason to believe that these mechanisms are exempt from change. This paper may, however, be considered to demonstrate the orderly nature of such changes and to outline the reasons why they may have occurred. The reasons may be expected to vary in relative importance from one instance to another.

**LITERATURE CITED**


