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The Flora of the Bonin (Ogasawara) Islands

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THE FLORA OF THE BONIN (OGASAWARA) ISLANDS: ENDEMISM AND DISPERSAL MODES[1]

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ABSTRACT

The Bonin (Ogasawara) Islands are an oceanic island group more than 1000 km from the Japanese Archipelago. As in other isolated islands of the Pacific Ocean, their flora is rich in endemic taxa. These endemics are mostly either schizo- or aneuendemics and have chromosome numbers that are either identical to or slightly different from those of their adjacent relatives. Three genera, *Callicarpa* (Verbenaceae), *Crepidiastrum* (Compositae), and *Pittosporum* (Pittosporaceae), are discussed as examples of adaptive radiation within the Bonin Islands. These genera are dispersed by birds, which swallow the seeds and later deposit them in new areas. Like plants with similar dispersal in the Hawaiian or Galapagos Islands, plants with bird-internal dispersal seem to have been the most successful in undergoing adaptive radiation into diverse habitats in the Bonin Islands.

Key words: Bonin Islands, endemism, aneuendemics, adaptive radiation, plant dispersal—birds, isozyme variation, *Callicarpa, Crepidiastrum, Pittosporum.*

INTRODUCTION

Island biotas, especially of isolated oceanic islands, commonly have large proportions of endemic taxa. These taxa have evolved in isolation over long periods of time, with very few possibilities for gene flow from other landmasses. They have become diversified into various habitats within the islands under conditions of ecological release. In other words, rapid adaptive radiation takes place on such isolated oceanic islands, resulting in biotas that are rich in endemic taxa (Carlquist 1974; Mervill 1979; Ono 1985).

The Bonin (Ogasawara) Islands comprise the southernmost territory of Japan. Located in the Pacific Ocean about 1000 km south of Tokyo, they were formed in the Tertiary (Asami 1970). The archipelago consists of 20 small islands scattered in the area of 26°30′ to 27°40′N and 142°00′ to 142°15′E. The islands are aggregated in groups known as, from north to south, Mukojima, Chichijima, and Hahajima (Fig. 1).

The climate of the islands is subtropical with an annual mean temperature of 23 C (mean of ten years from 1969 to 1978). No frost or snow has ever been recorded, and the temperature has never fallen below 5 C at any time throughout the year. The annual precipitation was less than 1300 mm for these ten years, and it seemed to be decreasing (Maejima and Oka 1980). Typhoons strike the islands almost every year, bringing heavy rain, which is important for the island biota. On the other hand, these typhoons cover almost entire islands with seawater spray for a day or more, often causing serious damage to both coastal and inland vegetation.

The Bonin Islands were discovered in the 16th century and later inhabited by both Japanese and European immigrants. The forests, dominated by subtropical

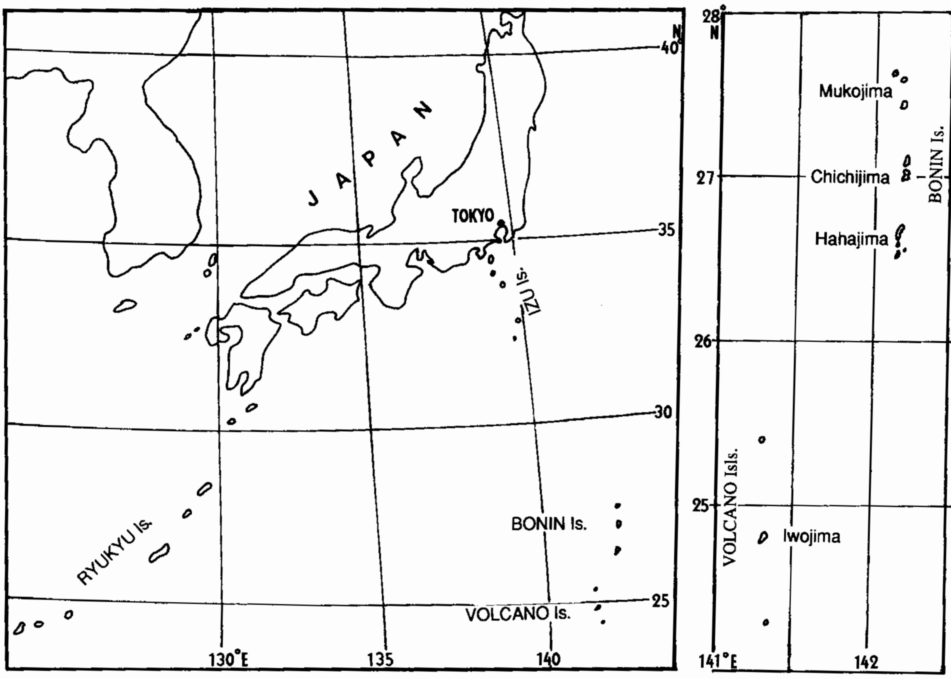


Fig. 1. *Left map*: Location of the Bonin (Ogasawara) Islands relative to the Ryukyu, Volcano, and Izu islands.—*Right map*: Relationship of the three Bonin Island groups: Mukojima, Chichijima, and Hahajima (above), and Iwojima of the Volcano Islands (below).

hardleaf evergreen trees and shrubs, were destroyed by cultivation and cattle grazing during the last century. Forest dominants included *Machilus* (Lauraceae), *Morus* (Moraceae), *Hibiscus* (Malvaceae), *Pouteria* (Sapotaceae), *Ochrosia* (Apocynaceae) and *Boninia* (Rutaceae). *Boninia* is one of the two endemic flowering plant genera of the archipelago.

FLORA OF THE BONIN ISLANDS

The Bonin Islands are more than 1000 km from adjacent landmasses and have always been isolated. Consequently, the level of endemism on the archipelago is proportionately high and the biota is relatively disharmonic. Yamazaki (1970) reported about 500 vascular plant species (including some varieties) on the islands; 43% of these were considered endemic. According to Tuyama (1970), more than 50% of the trees and shrubs are endemic. In our recent survey, more than 260 indigenous vascular plant taxa were recognized; 112 of these, about 43%, were considered to be endemic to the archipelago (Kobayashi and Ono 1987).

This high level of endemism is comparable to the levels found in the Galapagos Islands (Wiggins and Porter 1971) and the Hawaiian Islands (Carlquist 1974). On the other hand, every island of the Bonin Archipelago is very small and has very low relief, unlike these other island groups. Compared to the Hawaiian Islands, which have about 16,000 km^2 in total area and have a highest peak of 4100 m, or to the Galapagos Islands having an area of ca. 7700 km^2 and peaks higher than 1500 m, even Chichijima, the largest of the Bonin Islands, has an area of only ca. 24 km^2. The highest peak on the islands is only 498 m above sea level (Mt. Chibusa in Hahajima). The diversity of available habitats is therefore much lower in the Bonin Islands, compared with these other archipelagos, which also have a Tertiary origin and are isolated in the Pacific Ocean; the diversity of taxa is consequently also much lower.

The floristic origin of the Bonin Island flora is very complicated. Of approximately 500 indigenous taxa, the largest component of the flora has affinities with floras of southeastern tropical and subtropical Asia, such as the Philippines, Taiwan, and the Ryukyu (Lutchoo) Islands. Another major group is related to plants of Japan proper, especially of its southwestern portions, such as Kyushu, Shikoku, or the Izu Islands. Other components of the Bonin flora show affinities to floras of Hawaiian and/or other South Pacific or the Polynesian Islands; *Santalum* (Santalaceae), *Osteomeles* (Rosaceae), *Meterosideros* (Myrtaceae) and *Clinostigma* (Palmae) are examples. Finally, other taxa have affinities with the Mariana Islands flora, including several widespread pantropical species, such as *Canavalia lineata* DC., *Ipomoea pes-caprae* Sweet, and *Vitex rotundifolia* L. f.

CHROMOSOMAL DIFFERENTIATION

I have been studying the chromosome number diversity of the endemic flora of the Bonin Islands and comparing this diversity with that found in adjacent areas. Polyploidy is relatively rare in the Bonin Islands.

Favarger and Contandriopoulos (1961) proposed three categories to summarize the chromosome number diversity in isolated areas: patroendemics, apoendemics and schizoendemics. Patroendemics are diploid, whereas their more widespread counterparts are polyploid; they are thus relictual taxa that may now have a very restricted distribution. Patroendemics are therefore palaeoendemics. Apoendemics are auto- or allopolyploids of their relatives in adjacent or related areas; the polyploidy arose either after or during their migration to the area. Apoendemics are therefore neoendemics. Schizoendemics, the third category, do not differ in chromosome number from related taxa and grow sympatrically or parapatrically with their relatives in the same isolated area. Schizoendemics are therefore "active endemics"—specific or infraspecific differentiation either is taking place now or took place in the recent past by adaptive radiation and/or genetic drift.

I would like to add a fourth category, "aneuendemics," to include endemics that are undergoing active differentiation by aneuploid reduction or increase. All four categories are represented in the flora of the Bonin Islands. As one would expect, examples of patroendemics are quite rare in the flora; the islands are very isolated and of late Tertiary origin. The only known patroendemics in this flora are listed in Table 1.

Apoendemics, on the other hand, show widespread representation in the Islands (Table 1). In most cases, these taxa are tetraploid, while their adjacent relatives are diploid. There are a few triploid examples, however, such as *Wedelia biflora* and *Vaccinium boninense* Nakai (Ono 1975, 1977; Ono and Masuda 1981). *Wedelia biflora* is widely distributed on sandy beaches in tropical and subtropical Southeast Asia as well as among Pacific Islands. The Bonin Island populations of this species seem quite unstable; they grow only in a few places on the beaches of Mukojima and Hahajima. These populations are sometimes large and can propagate themselves vegetatively but they are often obliterated by tidal waves

Table 1. Examples of diploid chromosome numbers from each category of endemics in the Bonin Island flora. The chromosome number for each Bonin taxon is compared with the numbers that have been reported for its most closely allied congeners.

Endemic species in Bonin flora	2n	Related taxa	2n
ANEUENDEMICS			
Boehmeria boninensis Nakai	26	*B. longispica* Steud., most other spp.	28
Callicarpa glabra Koidz. [32, 34], *C. nishimurae* Koidz. [34], *C. subpubescens* Hook. & Arn. [30, 34]	30, 32, 34	*C. japonica* Thunb. [32, 36], *C. dichotoma* Raeusch. [36]	32, 36
Elaeagnus rotundata Nakai	18	*E. thunbergii* Serv.	28
Elaeocarpus photiniaefolius Hook. & Arn.	28	*E. hookerianus* Raoul	30
Euphorbia hirta L.	18	*E. hirta* (in India)	12, 20
Hedyotis grayi Bentham, *H. mexicana* (Hook. & Arn.) Hatusima	34	*Hedyotis*, other spp.	12, 18, 22, 36
Hibiscus glaber Matsum.	82	*H. tiliaceus* L.	80
Ligustrum micranthum Zucc.	48	*Ligustrum*, most spp.	46
Ochrosia nakaiana Koidz.	20	*O. oppositifolia* K. Schum.	22
Osteomeles lanata Nakai, *O. boninensis* Nakai	32	*O. schwerinae* C. K. Schneider	34
Malaxis boninensis (Koidz.) Nackejima [38], *M. hahajimensis* S. Kobayashi [36]	36, 38	*M. monophyllos* Sw.	30
Myoporum boninense Koidz.	68	*M. laetum* Forst. f.	108
Piper postelsianum Maxim.	26	*Piper*, other spp.	26, 48
Sapindus boninensis Tuyama	22	*Sapindus*, other spp.	30
Scutellaria longituba Koidz.	26	*S. scandens* D. Don	26
		Scutellaria, other spp.	22, 32, 34
Zanthoxylum arnottianum Maxim.	68	*Z. piperitum* DC.	70
APODENDEMICS			
Celtis boninensis Koidz.	40	*C. sinensis* Pers., in Japan	20
Fatsia oligocarpela (Nakai) Koidz.	48	*F. japonica* Decne. & Planch.	24, (48)
Morinda boninensis Ohwi	44	*Morinda*, 3 spp. in India	22
Peperomia boninsimensis Makino	110	*Peperomia*, most spp.	22, 44, 66
Pisonia umbellifera Seem.	±112	*P. brunoniana* Endl.	68
Rubus nishimuranus Koidz.	28	*R. hirsutus* Thunb., *R. trifidus* Thunb.	14
Sedum boninense Tuyama	44	*Sedum*, other spp.	16, 20, 22, 24, 30, 32, 48
Wedelia biflora DC.	45	*W. biflora*, other areas	30
PATROENDEMICS			
Alpinia boninsimensis Makino	36	*A. formosana* K. Schum., other spp.	48
Cirrhopetalum boninense Schlecht.	20	*Cirrhopetalum*, other spp.	38, 40
Trichosanthes boninensis Nakai	22	*T. cucumeroides* Maxim., in Japan	44

Table 1. Continued.

Endemic species in Bonin flora	2n	Related taxa	2n
Wahlenbergia marginata DC.	36	*W. marginata*, other areas	54, 72, 90
SCHIZOENDEMICS			
Calanthe hattorii Schlecht.	40	*Calanthe aristulifera* Reichb. f., most others	40
Cinnamomum pseudopedunculatum Hayata	24	*C. japonicum* Sieb.	24
Cirsium boninense Koidz.	34	*Cirsium*, most spp.	34, 68
Crepidiastrum ameristophyllum (Koidz.) Nakai, *C. grandicollum* (Koidz.) Nakai, *C. linguaefolium* (A. Gray) Nakai	10	*Crepidiastrum*, other spp.	10
Distylium lepidotum Nakai	24	*D. racemosum* Sieb. & Zucc.	24
Erythrina boninensis Tuyama	42	*E. indica* Lam.	42
Euonymus boninensis Koidz.	32	*E. japonicus* L.f.	32
Ficus boninsimae Koidz.	26	*Ficus*, other spp.	26, 52
Gardenia boninensis (Nakai) Tuyama	22	*G. jasminoides* Ellis	22
Goodyera boninensis Nakai	28	*G. hachijoensis* Yatabé [other spp.: 28–30]	28
Juniperus taxifolia Hook. & Arn.	22	*Juniperus*, most spp.	22
Osmanthus insularis Koidz.	46	*O. fragrans* Lour.	46
Pittosporum boninense Koidz., *P. chichijimense* Nakai, *P. parvifolium* Hayata	24	*P. tobira* Dryand. in Ait.	24
Psychotria boninensis Nakai	22	*Psychotria*, most spp.	22
Schima mertensiana (Sieb. & Zucc.) Koidz.	36	*S. wallichii* Choisy	36
Sciaphila okabeana Tuyama	48	*S. japonica* Makino	48
Symplocos pergracilis (Nakai) Yamazaki	22	*Symplocos*, most spp.	22
Tarenna subsessilis (A. Gray) Ohwi	22	*T. littoralis* Merrill	22
Trachelospermum foetidum Nakai	20	*T. jasminoides* Lem.	20
Viburnum boninsimense (Makino) Koidz.	18	*Viburnum*, most spp.	18
Wikstroemia pseudoretusa Koidz.	18	*Wikstroemia*, most spp.	18

from typhoons. Seeds, likely produced by agamospermy, are also produced. In the case of *Peperomia,* the unique endemic species of the islands is *P. boninsimensis,* which has $2n =$ ca. 110. In most species of this genus, somatic chromosome numbers of $2n = 22$, 24, 44, and 66 occur (Fedrov 1969). Based on these reports, the Bonin species very likely is a decaploid, a very rare condition for the genus (Ono 1977).

Schizoendemics are the best-represented category of the Bonin endemics (Table 1). My proposed category, "aneuendemics," also includes numerous taxa, as shown in Table 1. In conclusion, speciation on the Bonin Islands has rarely been associated with polyploidy, although several cases of aneuploidy are known.

SOME EXAMPLES OF ADAPTIVE RADIATION

As pointed out by Carlquist (1974) and many other botanists, a most important phenomenon in an isolated island, or especially in an archipelago, is adaptive radiation within the island(s) while it is in a condition of ecological release. An original immigrant taxon, once successful in establishing itself on the island, could then disperse to various open adjacent habitats without competition from other taxa. The Bonin Islands, however, are very small and have fewer and lower mountains, so the habitat diversity is lower than that present on the Hawaiian or Galapagos Islands; the opportunities for adaptive radiation are correspondingly lower. Nevertheless, we have observed several good examples of adaptive radiation on the Bonin Islands, as illustrated by the following three examples.

Pittosporum

In the Bonin Islands, four species of *Pittosporum* have been described. *Pittosporum* has only one species, *P. tobira* Ait., throughout the Japanese Archipelago, including the Ryukyu (Lutchoo) Islands, although some botanists have treated the Ryukyu plants as *P. lutchuense* Koidz. In contrast, there are four species of *Pittosporum* in the Bonin Islands: *P. boninense, P. chichijimense, P. parvifolium* Hayata, and *P. beecheyi* Tuyama. The morphological characteristics of these, as well as their preferred habitat and chromosome number, are shown on Figure 2. My research on peroxidase isozyme variation showed that *P. boninense,* the most widespread of these species, is also the most genetically uniform (Ono 1985). On the other hand, the other three species, which have very restricted distributions, have uniquely different isozyme variation patterns. Consequently, I assume they differentiated prior to the arrival of *P. boninense* in the islands.

According to Carlquist (1974), flowering plants of oceanic islands commonly have seeds and/or fruits that are large in size, but small in number. *Pittosporum boninense* produces a comparatively large number of fruits and seeds, both of which are smaller in size than those produced by the other three species, which produce fewer seeds. This supports my assumption that this species is a later immigrant to the Bonin Islands.

Callicarpa

Three species of *Callicarpa* are endemic to the Bonin Islands, *C. glabra, C. nishimurae,* and *C. subpubescens.* The last species has the widest distribution in the islands and occupies rather wet habitats in the tall evergreen forests in Chichijima; in Hahajima, it grows in various habitats from coastal scrub areas up to higher montane mist forests. The other two species are restricted to specific habitats in Chichijima; *C. glabra* is found in dry sunny forest margins, whereas *C. nishimurae* is known only from very dry windy hilltops. Kawakubo (1988) reported that the three species are quite uniform on Chichijima, but that *C. subpubescens* is rather variable in Hahajima, spanning the entire range of variation for morphological characters of the three species. He concluded that *C. subpubescens* is probably the youngest of the three taxa, and that speciation is especially

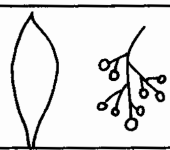
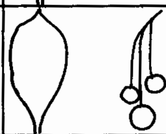
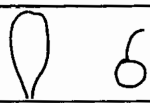
SPECIES	HABIT	HABITAT	CHARACTERISTICS: Leaf shape, Inflorescence (fruiting)	CHROMOSOME NUMBER (2n)	DISTRIBUTION: Anijima	Chichijima	Hahajima	Mukojima	Anejima	Imotojima	Meijima
P. boninense	Tree	Montane		24	*	*	*				
P. chichijimense	Tree	Inland		24		*					
P. parvifolium	Shrub	Hilltop		24		*					
P. beecheyi	Shrub	Coastal		24			*	*	*	*	*

Fig. 2. A comparison of the four species of *Pittosporum* endemic to the Bonin Islands (Ono 1985). *Pittosporum beecheyi* is scattered on several islands of the Hahajima Group; these small islands are close to each other and historically have been connected to Hahajima.

active in Hahajima, where as yet no related taxa have migrated, and where ecological niches are still empty. He also concluded that sexual differentiation, including functional monoecy, has been developing in this group and has been important in their speciation. These species have unstable chromosome numbers; somatic numbers of $2n = 30$, 32, and 34 have been counted from a single population (Ono 1975). This also suggests that they are still actively speciating.

Crepidiastrum

A small east Asian genus of Compositae, tribe Chichorieae, *Crepidiastrum* includes about ten species found in the Japanese Archipelago, Korea, Taiwan, and the Bonin Islands. Three species, *C. ameristophyllum, C. grandicollum,* and *C. linguaefolium,* are known from the Bonin Islands, where each is endemic to a separate restricted area and endangered. *Crepidiastrum grandicollum* is a herbaceous perennial about 10–30 cm tall, whereas the other two species are woody with soft, semisucculent stems less than 1 m tall. All have $2n = 10$ somatic chromosomes that are large, more than 10 μ long. Isozyme patterns for ten enzymes were compared by Itow and Ono (1989) for these taxa and their counterparts on the Japanese Archipelago. The result of this study showed that the Bonin species are more closely related to each other than any are to the Japanese species. The genetic distance was estimated on this isozyme similarity (Fig. 3).

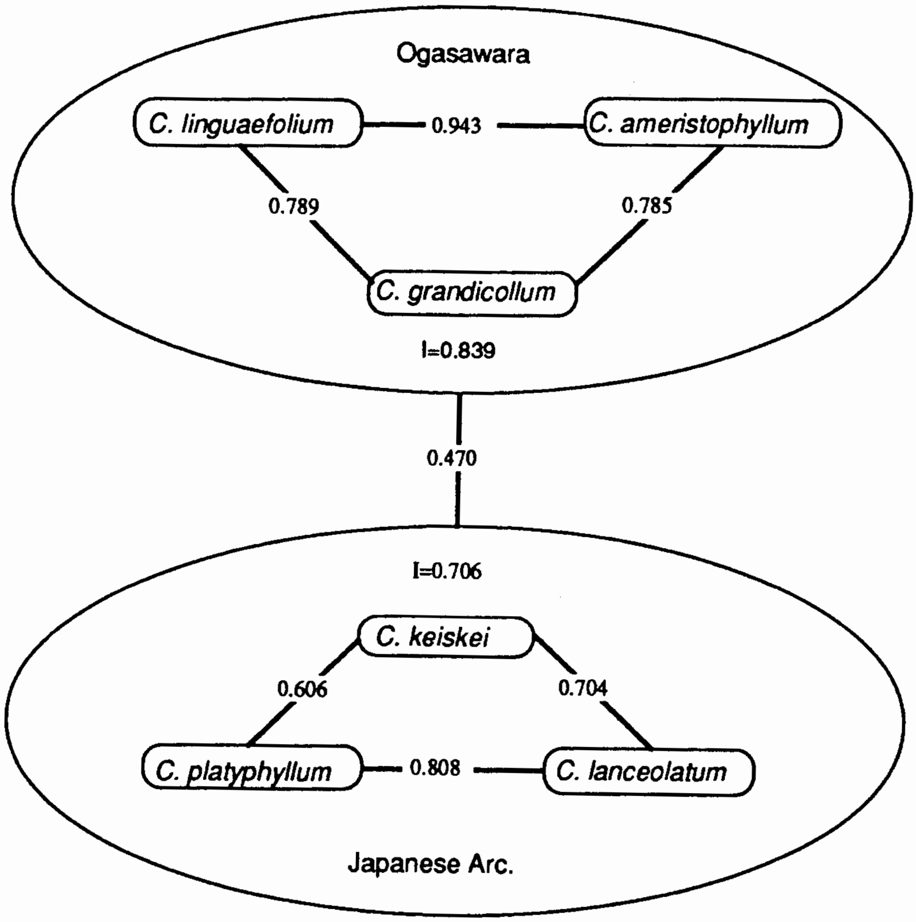


Fig. 3. Genetic identities among the Bonin species of *Crepidiastrum* and their counterparts in the Japanese archipelago.

MODE OF DISPERSAL

Nearly all of the indigenous plants of the Bonin Islands are descendants of migrated ancestors that reached the island by long-distance dispersal over more than 1000 km of open ocean. As mentioned in the Introduction, these taxa are related to species of Southeast Asia, the Japanese Archipelago, the Marianas and neighboring Pacific islands, and, even further away, the Hawaiian Islands or Australia.

More than 70% of the indigenous flowering plants of the Bonin Islands are dispersed by birds, especially via internal transport of seeds. Seeds are eaten and are carried within the gut of the bird, exemplifying "BI" dispersal (Carlquist 1974). This proportion is similar to that found in other Pacific islands (Fig. 4). On the other hand, 16% of the indigenous taxa of the Bonin Islands are wind-dispersed, compared with values of only 2–5% for the other islands (Carlquist 1974; Ono and Sugawara 1981). A similarly high proportion of anemochory is found in the flora of Samoa, which is also in the far western portion of the Pacific Ocean.

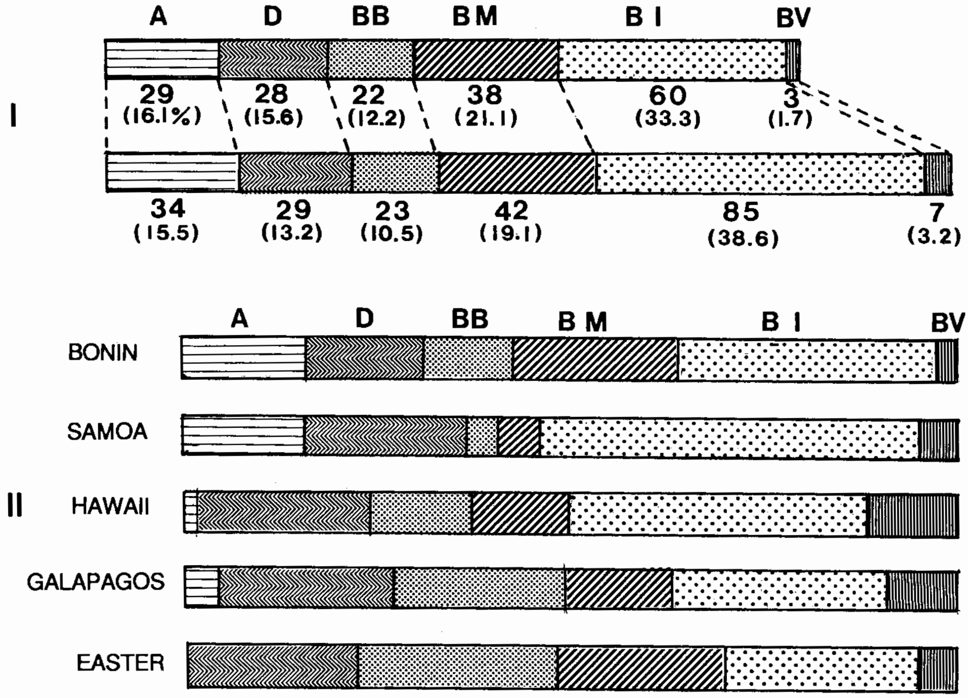


Fig. 4. Comparison of angiosperm floras according to modes of dispersal.—I. Comparison of estimated numbers of ancestors assumed to have migrated (upper bar) and actual numbers of indigenous taxa examined (lower bar).—II. Comparison of dispersal modes for plants of several Pacific island floras (Ono 1985).—A. Wind.—D. Drift by ocean currents.—BB. Mechanical attachment to bird feathers.—BM. Embedded in mud on bird feet.—BI. Eaten by birds and carried internally.—BV. Fruits or seeds externally attached to birds by viscous substances.

Dispersal by western winds or typhoons from adjacent islands or landmasses to the east would be possible here. On the other hand, the Galapagos, Juan Fernandez, or Easter Islands, or even the Hawaiian Islands, all show low proportions of taxa with wind dispersal in their floras and are located in the eastern part of the Pacific Ocean, with a vast expanse of unbroken ocean to the west.

The three genera of plants mentioned above as examples of adaptive radiation within the Bonin Islands (*Callicarpa, Crepidiastrum,* and *Pittosporum*) have bird-mediated dispersal of the BI type. Within the floras of other isolated islands of the Pacific, the most remarkable cases of adaptive radiation also involve species with bird-dependent dispersal (Table 2). Bird dispersal is apparently an advantageous condition for plant speciation on these islands.

How can this advantage be explained? Bird-dispersed plants are more likely to be randomly dispersed over various habitats than plants that have other means of dispersal. The intestine of birds is short, so seeds and fruits are digested for only a few hours before defecation (Cain 1971, etc.). A colonizing immigrant species would disperse its seeds via birds to other neighboring habitats. These new habitats would be open for colonization, due to ecological release.

In contrast, plants with other modes of dispersal, such as via ocean currents, could disperse only to similar habitats, habitats that would not place selective

Table 2. Lists of genera that have speciated extensively within three island groups, indicating modes of dispersal (Ono 1985). Abbreviations for dispersal modes are given in the caption for Figure 4. Data from Carlquist (1974), Ono and Sugawara (1981), and Wiggins and Porter (1971).

Islands	Genus	Family	Estimated number of original immigrants	Actual number of endemic species	Mode of dispersal
Hawaii	*Cyrtandra*	Gesneriaceae	1	130	BI
	Hedyotis	Rubiaceae	1	50	BI/(BM)
	Peperomia	Piperaceae	1	48	BV
	Cyanea	Campanulaceae	1	48	BI/BV
	Labordia	Loagniaceae	1	40	BI
	Phyllostegia	Labiatae	1	40	BI
	Stenogyne	Labiatae	1	40	BI
	Palea	Urticaceae	1	40	BI
	Schidea	Caryophyllaceae	1	32	BM
	Pittosporum	Pittosporaceae	1	30	BV
Galapagos	*Opuntia*	Cactaceae	1	17	BI
	Alternanthera	Amaranthaceae	1	15	BI/BB
	Scalesia	Compositae	1	12	BI/(BB)
	Acalypha	Euphorbiaceae	1	9	BI/BB
	Mollugo	Aizoaceae	1	9	BI/BM
	Peperomia	Piperaceae	1	5	BV
Bonin	*Pittosporum*	Pittosporaceae	1	4	BV
	Symplocos	Symplocaceae	1	3	BI
	Callicarpa	Verbenaceae	1	3	BI
	Ilex	Moraceae	1	3	BI
	Ficus	Moraceae	1	3	BI
	Machilus	Lauraceae	1	3	BI

pressures on either morphological or ecological features of the plants. Even certain bird-dispersal modes show this difficulty: plants with minute seeds or achenes that are transported with mud on the feet of sea birds (the "BM" type of Carlquist) are also dispersed to similar habitats, such as marshes or lagoons. Consequently, they are not exposed to the diversity of habitats confronted by the progeny of plants with BI dispersal.

In conclusion, bird-internal dispersal may accelerate the adaptive radiation of plants after they migrate to an isolated island or island group with various diversified habitats, as long as ecological niches remain unoccupied. We see good examples of this in the conspicuous adaptive radiation demonstrated by *Cyrtandra* (Gesneriaceae, ca. 130 spp.), *Hedyotis* (Rubiaceae, ca. 50 spp.), *Peperomia* (Piperaceae, 48 spp.), etc., in the Hawaiian Islands, and *Opuntia* (Cactaceae, ca. 17 spp.) and *Scalesia* (Compositae, ca. 13 spp.) in the Galapagos Islands. Even in the Bonin Islands, where the diversity of habitats is much lower, all of the genera that have differentiated into more than three species have BI dispersal.

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FOOTNOTE

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