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SUPPORT FOR BAKER'S LAW—AS A RULE

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In a very interesting book and a series of articles (two of which have appeared in this journal) Sherwin Carlquist (1965, 1966*a, b, c, d*) has published his views on the biota of long-distance dispersal, giving special attention to the problems posed by the floras of oceanic islands. I can concur heartily with the great majority of the conclusions which he draws and I believe that these publications represent a notable contribution to our understanding of waif floras in general. But there are some points of disagreement.

Thus, Carlquist (1966*d*:443) asserts that "the value of dioecism in insular circumstances is so great that the necessity for simultaneous introduction and establishment of at least two propagules is not a severe disadvantage. As suggested earlier (Carlquist, 1965, 1966*a*), this disadvantage is probably more imaginary than real . . ." I believe that these words are too strong. Also, I disagree that "If dioecious stocks immigrated to the [Hawaiian] Islands, "Baker's Law" must, in part, be abandoned" (Carlquist, 1966*d*:442).

"Baker's Law" was so called by Stebbins (1957:344). The basic statement of the principle is given in Baker (1955). The interpretation which is given to it in Carlquist's papers (e.g., 1966*a*:262) is considerably more rigid than suggested by Baker or by Stebbins. Thus, Baker's (1955) statement is "With self-compatible individuals a single propagule is sufficient to start a sexually-reproducing colony (after long-distance dispersal), making its establishment much more likely than if the chance of two self-incompatible yet cross-compatible individuals sufficiently close together spatially and temporally is required. . . . [while] with plants apomixis and purely vegetative reproduction are also available to replace self-incompatible hermaphroditism (and monoecism) or dioecism." There is nothing so absolute here that the occasional successful establishment of a dioecious stock in Hawaii should cause the abandonment of any part of the principle.

It is Carlquist's thesis that an outbreeding system is needed to maximize variability in the progeny from the limited number of immigrant plants. Then, if it is true that, as Carlquist claims, the necessity of simultaneous introduction onto an oceanic island (in relatively close proximity) of two appropriate propagules is not a

serious disadvantage to a dioecious species, it should be even less disadvantageous for a hermaphrodite (monoclinous) species showing self-incompatibility, for here (with all kinds of incompatibility systems known, except that of distyly) the chances are greater that the two adjacent plants will be cross-compatible than that they will be cross-incompatible. For dioecious species, the chances are no more than even that they will be of the same or of different "sex."

Consequently, if Carlquist's argument is justified, we might expect that there would be a higher than usual proportion of self-incompatible species on oceanic islands. However, Rick (1966) tested species native to the Galápagos Islands and found an indication of a relatively low frequency of self-incompatibility in that flora. Carlquist (1966*d*) reported that a species of *Wilkesia* from Hawaii appeared to be self-incompatible when cultivated in California but he has told me that other isolated plants grown in Germany have set seed. He lists one other taxon (*Hesperomannia*) as self-incompatible and another (*Planchonella*) is included with a question mark. The results of tests on further taxa will be awaited with interest, bearing in mind that more is required in the test than noting that an isolated plant growing away from its native habitat does not set seed, for which reason the acquisition of sufficient data to estimate the frequency of self-incompatibility will be a long task.

A short cut is provided by genera in which heterostyly is found. Except in the Boraginaceae, heterostyly has always been found to be associated with some degree of self-incompatibility thus providing an easily visible marker for it. Therefore, it is of interest that Carlquist (1966*d*:447) writes "Heterostyly is not, apparently, present in the Hawaiian flora," retracting an earlier statement (Carlquist, 1965:269) that it is present in at least six genera. This apparent absence of heterostyly is especially important because the Hawaiian flora contains genera which, elsewhere at least, show heterostyly with accompanying self-incompatibility, e.g., *Psychotria* (Ernst, 1932; Bremekamp, 1934; Baker, 1958) and *Plumbago* (Dahlgren, 1918; Baker, 1966). Carlquist (1966*a, d*) has twice presented a series of percentages derived from my work with *Limonium* (Plumbaginaceae) to suggest that self-incompatibility is more advantageous than self-compatibility for species reaching oceanic islands. However, the

islands concerned are in the Atlantic Ocean, with most of the species on the Canary Islands, the nearest of which is only 40 miles from the African mainland. Some of the special conditions applying in these cases were pointed out in Baker (1953) and will also be discussed elsewhere. They need not be detailed here.

Consequently, unless a rather high proportion of the Hawaiian taxa so far examined prove to be self-incompatible when they are studied, there seems to be no reason to suppose that the mass of species with hermaphrodite (monoclinous) flowers in the Hawaiian flora will give us cause to abandon the belief that self-compatible (rather than self-incompatible) taxa are favored in establishment after long-distance dispersal (i.e., "Baker's Law"). Neither is there any reason to suppose that of the clinous species the monoecious ones will prove incapable of self-pollination, for self-incompatibility is almost unknown in monoecious taxa (Godley, 1955).

Any case for abandoning "Baker's Law," therefore, must rest upon the dioecious species in the Hawaiian flora—and here there is an impressive array. By Carlquist's (1966*d*:440) estimate there are 27.5% of dioecious species in the Hawaiian flora, a proportion which exceeds any other yet calculated, surpassing the 13.5% (Godley, in Hair, 1966) or 14.5% (Carlquist, 1966*d*) for the New Zealand flora (the figure of 25% in Carlquist, 1965:268, apparently includes monoecious species) and to be compared with only 3.1% for the British flora (McCob, 1966) and 2.6% for the California flora (Baker, unpub.). Dioecism could have been present in the immigrant stocks or have developed after establishment of the stock in the Islands. Only the former would be offenders against the spirit of "Baker's Law." Carlquist (1966*d*:440-3) lists 10 cases where it is likely that an immigrant came from a dioecious stock.

Fosberg (1948) estimated that about 272 immigrants are the minimum number required to give rise to the 1400 to 2000 species of flowering plants in the Hawaiian flora; 10 out of 272 is 3.7%. Considering that the Hawaiian flora is exclusively perennial and very woody this is not a strikingly high proportion. With long-lived perennials there is less need for contemporaneity in the arrival of the propagules that produce the staminate and pistillate plants which must be present for the formation of seeds; the possession of powers of vegetative reproduction helps still more.

An important consideration is the notorious infrequency of dioecism where it occurs among flowering plants. Even in families such as the Salicaceae, where dioecism is deeply ingrained, monoecious trees occur occasionally. *Astelia* (Liliaceae) is one of the genera quoted by Carlquist (1966*d*:442) as undoubtedly arriving in

Hawaii in the dioecious condition, but Moore (1966) has shown (for New Zealand species of this genus, at any rate) that hermaphrodite flowers occur on some plants and produce germinable seed (even pistillate flowers on isolated plants produce some seed, apparently by apomixis). There are suggestions in the older literature of polygamous flower distribution in some other of the genera concerned (e.g., *Eurya* and *Xylosma*) but these, of course, should not be accepted without checking on an abundance of living material. The chances of seed being set by isolated plants in any taxon is greatly increased by repeated flowering; all of the Hawaiian plants are perennial.

Additionally, of the remaining taxa which may have become established in Hawaii despite arrival in the dioecious condition, at least *Pandanus* may represent a special case where the unit of dispersal is a multi-seeded fruit rather than an individual seed (see Baker, in Raven, 1963:154). Clearly, the difficulty of establishing the necessary adjacent staminate and pistillate plants is less for such taxa than for those in which seeds are dispersed individually. In the case of *Pandanus* these fruits might have been brought to the islands by man, cf. Guppy (1906:53, 158, 552), Degener (1930:48) and Selling (1947:341). Interestingly, Rock (1913) comments on the rarity of staminate plants of *P. odoratissimus*. L.f., which suggests that the possibility of facultative apomixis in this plant should be investigated, especially as Skottsberg (1955) has recorded the odd chromosome numbers $2n = 51, 54$, and 60 for the synonymous *P. tectorius* var. *sandviicensis* Warb.

An interesting case, apparently in line with the belief that dioecism *does* pose problems for establishment after long-distance dispersal, is provided by *Fragaria chiloensis* (L.) Duchne. This species, abundant along the Pacific coasts of North and South America, is characteristically dioecious. However, the material which grows on the mountains of the Hawaiian Islands bears hermaphrodite, presumably self-compatible flowers (Carlquist, 1966*d*:439).

For the great majority of the Hawaiian dioecious species there is no reason to suppose that they did not develop their dioecism *after* the arrival of their ancestors in the Islands—and the special interest of this is that not only is such an evolutionary development not in disagreement with "Baker's Law," it can be shown actually to substantiate it. A high proportion of dioecism in a flora is what would be expected if there is a selective pressure favoring outcrossing but a shortage of self-incompatibility to enforce it (a shortage which would be the result of discrimination in favor of self-compatible taxa among the immigrants).

Dioecism is a less efficient outcrossing system

than self-incompatibility. In the first place, only the pistillate plants set any seed; furthermore, adjacent plants are as likely to be of the same "sex" as of opposite "sexes." Heterostylous systems are slightly more efficient than dioecism in that all plants are capable of bearing seed, but the most efficient systems are the multiple allele homomorphic systems where every plant is a seed-setter and likely to be cross-compatible with its neighbor.

In the angiosperms as a whole there is a strong *inverse* correlation between the occurrence of dioecism in a family (or section of a family) and the occurrence of a self-incompatibility system (Baker, 1959). This becomes almost complete at the genus level. Notable for repeated "experiments" with dioecism, for example, is the Caryophyllaceae—in which genes for the establishment of a self-incompatibility system may not exist (and, certainly, none has been reported). Thus, dioecism in angiosperms may be looked upon as a poor substitute for self-incompatibility and the latter may be expected to show preferential adoption.

However, if immigrants to Hawaii were self-compatible (and "Baker's Law" suggests that they would tend to be), any selection pressure for outcrossing subsequent to their arrival would demand either the autochthonous development of a self-incompatibility system or else the development of a less efficient substitute outcrossing system such as dioecism. But the evolution of a self-incompatibility system is a very rare event and the evolution of a multiple allele system, in particular, is an exceedingly unlikely event (see Whitehouse, 1950, for the reasons)—so unlikely that Lewis and Crowe (1958) consider that in all cases where two closely related taxa are respectively self-incompatible and self-compatible, the latter may be presumed to be derived from the former. The breakdown of an incompatibility system, giving self-compatibility, can take place (and has been observed to take place) with a single-gene mutation (Lewis, 1954; etc.), but the build-up of such a system is an extremely complicated and unlikely occurrence.

By contrast, dioecism is relatively easily established. Physiologically it may involve no more than an alteration of the auxin balance in the inflorescence (Heslop-Harrison, 1957; etc.); genetically it can be achieved rather simply, using only genes with alternative rather than multiple alleles (Baker, 1959:179).

Consequently, the most likely interpretation of the high proportion of dioecism in the Hawaiian (and New Zealand) flora is that it is imperfectly developed in most genera and, in those, it has mostly been derived autochthonously in response to a selective pressure for outcrossing applied to hermaphrodite or monoecious taxa which had arrived unarmed with any self-incompatibility.

Protandry, protogyny, gynodioecism, and other "mechanical" aids to outcrossing may also be evolved and selected for in these circumstances, and they are found in impressive proportions in the Hawaiian flora (Carlquist, 1965, 1966b). None of these aids to outcrossing can match self-incompatibility in efficiency (some do not even prevent geitonogamy—the cross-fertilization of flowers on the same plant); consequently, their very abundance in the Hawaiian flora carries a strong implication that the original immigrants were self-compatible.

It is possible to illustrate the evolutionary sequence that I postulate with an example from the Plumbaginaceae (Baker, 1966). In Europe, *Armeria maritima* (Mill.) Willd. bears showy flowers and is completely self-incompatible (with a heteromorphic incompatibility system) but, in migrating to the New World (a process which probably involved some "long-distance" dispersal) through arctic regions, it lost its self-incompatibility. Monomorphic, less showy, self-compatible plants occur in the arctic where there is some shortage of potential pollinators. Farther south, however, along the California coast, anthophilous insects are plentiful and outcrossing becomes feasible (and probably advantageous). However, the *Armeria* had lost its self-incompatibility—but it could produce showy flowers (and *A. maritima* var. *californica* Lawr. has them) and it could adopt a substitute method of enforcing outcrossing—gynodioecism. In fact, gynodioecism has become an obvious feature of many California populations of this taxon.

In their studies of the pollination relationships of the Galápagos flora, Rick (1966) and Linsley, Rick, and Stephens (1966) have shown that the earlier immigrants were probably highly autogamous; subsequent immigrants have been able to make use of the endemic carpenter bee, butterflies, and hawkmoths in pollination (but still with no evidence of self-incompatibility). We may visualize the same sequence for the Hawaiian flora with, however, a relative abundance of anthophilous insects and birds permitting even the evolution of dioecism and associated floral states which increase the possibilities of outcrossing. But "Baker's Law" is observed—as a rule.

One final point needs to be made. Although, with self-compatibility, a seed-producing colony *can* be started from a single seed, a subscriber to "Baker's Law" does not need to believe that all populations developing after long-distance dispersal always are the result of the introduction of only one seed. Multiple introductions can occur and provide genetical variability. The important point is that self-compatibility in the immigrants means that the several propagules do not all have to arrive at the same time, nor do the resulting plants have to become established in

close proximity to each other. Self-compatibility allows each immigrant plant the chance of multiplying, so that it may form a population and even spread, thereby raising the chance of its meeting another one of the same taxon (with beneficial intercourse to follow).

Clearly, the greatest need in this area of biology is for further field and experimental studies (by as many workers as can spare the time) on the reproductive biology of the plants which make up floras of all kinds—colonizing, stable, or relictual. Several colleagues in various institutions who are engaged in assembling this kind of information have given me the benefit of their counsel during my preparation of this paper; I am most grateful to them.

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