Additional Experimental Crosses in Hawaiian Bidens (Asteraceae)1

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FOR THE PAST 35 YEARS the phenomenon of natural hybridization has been linked with Hawaiian Bidens, mostly through the energetic and discerning fieldwork of Otto Degener. Several natural hybrids were reported by Sherff (1937), based on the collections of Degener and others. The list of putative natural hybrids was extended to 16 by Gillett and Lim (1970). The latter paper reported some 23 different experimental F₁ hybrids, indicating weak to nonexistent genetic barriers between species and giving a general confirmation to the field and herbarium studies of hybridization. The purpose of this paper is to record additional experimental hybrids in Hawaiian Bidens, some of these involving two species (B. fulvescens and B. skottsbergii) which gave poor indications of interspecific hybridizations in the earlier crossing program.

Hawaiian Bidens have sterile "ray" flowers, so that only the "disc" flowers are involved in producing achenes. In a given plant, the "disc" flowers may be bisexual or unisexual (female). Most species are characterized by bisexual plants. However, B. fulvescens, B. menziesii, and B. skottsbergii are gynodioecious, possessing bisexual individuals and female individuals. Therefore, these three species are relatively easy to work with in experimental cross-pollinations because it is possible to transfer pollen to female plants without the complications of accidental self-pollination by the female parent. This highly favorable circumstance facilitated five of the seven successful experimental crosses reported herein.

The six species utilized in this crossing program are as follows:

Bidens skottsbergii Sherff. Gillett 1753. Hawaii. Erect shrub about 2 m high growing on the 1750 lava flow about 0.5 miles from the coast and 2.5 miles (4.0 km) east of Black Sand Beach. Associated plants include *Metrosideros*, *Scaevola taccada*, and *Polypodium*. Elev. 12 m.

Bidens menziesii var. filiformis (Gray) Sherff. Gillett 1756. Hawaii. Erect shrub 2–4 m high growing on the south slopes of Mauna Kea in dry land shrub vegetation including Dodonaea, Osteomeles, Dubautia, and mixed grasses. Elev. 1.800 m.

Bidens mauiensis var. cuneatoides (Gray) Sherff. Gillett 1873. West Maui. Decumbent herb growing on the sand hills near Waihee, with Lipochaeta, Scaevola coriacea, Nama, Fimbristylis, and associated dune vegetation. About 500 m from the sea, elev. 20 m.

Bidens mauiensis var. mauiensis (Gray) Sherff. Gillett 1872. East Maui. Decumbent herb growing on the south slope of Mt. Haleakala at the bridge over Manawainui Gulch, 10 miles (17 km) west of Manawainui Stream. Dry land vegetation including Euphorbia and associated weeds. About 300 m from the sea, elev. 60 m.

Bidens fulvescens Sherff. Gillett 2144. Oahu. Herb to low shrub up to 2 m high growing along the Mokuleia trail above Peacock Flat, western Waianae Range. Associated plants include Acacia koa, Metrosideros, Charpentiera, Pisonia, Styphelia, and Wikstroemia. Elev. 600 m

Bidens molokaiensis (Hillebr.) Sherff. Gillett 1807. Molokai. Creeping herb growing on the windswept crest of the north coast headland near Hoolehua, in the Hoolehua city dump. Associated plants include Lipochaeta, Cynodon (Bermuda Grass), and various weeds. Elev. 150 m.

Anthesis in the bisexual "disc" flower of *Bidens* is marked by the upward thrust of the closely appressed stigmatic branches through the cylinder of dehisced anthers and the elevation of the pollen mass above the open, nectar-filled corolla. In making experimental cross-pollinations, an individual pollen-bearing style is re-

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moved with microforceps and is utilized as a "pollen brush" in pollinating the selected female parent. Most successful pollinations are accomplished when the style branches of the female parent have separated and each branch has just completed a recurvature of approximately 180°. A head magnifier was utilized to accomplish the pollen transfer precisely into the cleft and inner surfaces of the style branches.

This report deals largely with positive evidence. Unsuccessful crosses constitute inconclusive evidence, for the failure to obtain a hybrid may well be due to inadequate experimental manipulation rather than to any genetic barrier. Also, failure to obtain germination from hybrid achenes might occur because of inadequate provisions for germination rather than because of inviable hybrid embryos.

A successful hybridization was confirmed by scoring the presumed hybrid against the selfed progeny of the female parent.

All of the F_1 hybrids, with one exception, were of approximately intermediate morphology. The exception involves the cross between the male *Bidens mauiensis* var. *cuneatoides* and the female *B. molokaiensis*. The two hybrid plants reflect the facies of the female parent (matricliny) as opposed to the approximately intermediate status of two other hybrids obtained from the reciprocal cross.

Considering the above precautionary measures in the assignment of interspecific hybrids, I feel that the total picture of compatibility developed from these studies undoubtedly is on the conservative side.

Vouchers of parents and experimental hybrids are deposited in the herbaria of the Bernice P. Bishop Museum and the University of California at Berkeley, as well as in the Herbarium of the University of California at Riverside.

The results of this crossing program are depicted in the crossing polygon of Fig. 1. With-

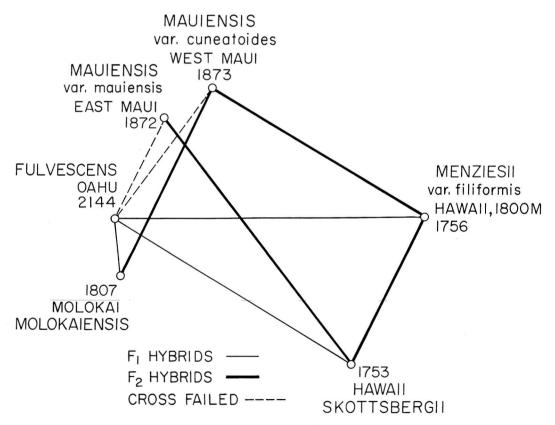


Fig. 1. Experimental crosses accomplished in Hawaiian Bidens, 1970-1971.

TABLE 1

PUTATIVE NATURAL HYBRIDS OF HAWAHAN Bidens SUPPORTED BY EXPERIMENTAL HYBRIDIZATIONS

HYBRID PARENTAGE*	ISLAND ON WHICH PUTATIVE HYBRIDS OCCUR				
	OAHU	MOLOKAI	LANAI	WEST MAUI	HAWAII
B. hillebrandiana (Molokai, Maui, Hawaii)					
× B. weibkei (Molokai)	×				
B. coartata (Oahu) X B. molokaiensis (Molokai)	×				
B. hillebrandiana X B. mauiensis var. cuneatoides (W. Maui)	1			×	
B. macrocarpa (Oahu) × B. weibkei				×	
B. menziesii var. filiformis (Molokai, Maui, Hawaii)					
× B. mauiensis var. cuneatoides			×	×	
B. coartata × B. skottsbergii (Hawaii)			×	×	
B. menziesii var. menziesii (Molokai, Maui, Hawaii)					
× B. weibkei		×	×		
B. ctenophylla (Hawaii) $ imes$ B. menziessii var. filiformis					×
B. mauiensis var. cuneatoides × B. molokainesis	×				
B. skottsbergii × B. menziesii var. filiformis				×	×

^{*} Distribution of parent in parentheses.

out exception the hybrids portrayed in this diagram were robust, vigorous plants. Two hybrids of *Bidens fulvescens* parentage (to *B. molokaiensis* and *B. skottsbergii*) had not flowered after nearly a year of growth. However, the remaining three hybrids flowered and produced abundant achenes between 8 and 10 months after germination.

Earlier experimental work (Gillett and Lim, 1970) supported a total of eight putative natural hybrids. These and two additional natural hybrids supported by the current paper are listed in Table 1.

The last natural hybrid listed in Table 1 is one of the most significant in that it combines two species with vastly contrasting adaptive norms. The majority, and possibly all populations of *Bidens skottsbergii*, grow relatively close to the sea in frost-free habitats. By contrast, *B. menziesii* var. *filiformis* occurs at higher elevations (1,800 m) than any other Hawaiian *Bidens* and is subjected to winter frosts. This is in addition—to—various—morphological—contrasts which are very great between the two species.

It is clear from the 10 natural hybrids cited in Table 1, all supported by experimental evidence of genetic compatibility between the respective putative parents, that there has been considerable interisland dispersal of *Bidens* species in the Hawaiian Islands. Only two of the 10 taxa involved in these natural hybridizations have fruits with well-developed, retrorsely-barbed

awns that could relate to the speculation of achene transport via adherence to the feathers of birds. The remaining eight species have awnless achenes or achenes with such rudimentary awns that to assume their adherence to feathers and resultant transport by birds would be excessively speculative. There is little doubt that these species with awnless achenes have accomplished very effective dispersal, but the dynamics of this dispersal are obscure.

The relatively broad expression of natural hybridizations portrayed by the above evidence would indicate that hybridization is perhaps a basic evolutionary process in Hawaiian *Bidens*. The interpretation of this, involving the conversion of closed, small, founder populations into open, larger populations through the development of an outcrossing system and selection against genetic barriers has been outlined in earlier work (Gillett, in press).

LITERATURE CITED

GILLETT, G. W. In press. *In* D. H. Valentine [ed.] Taxonomy and phytogeography of flowering plants in relation to evolution. Academic Press, New York.

GILLETT, G. W., and ELVERA K. S. LIM. 1970. An experimental study of the genus *Bidens* in the Hawaiian Islands. Univ. Calif. Publ. Bot., 56:1–63.

SHERFF, E. E. 1937. The genus *Bidens*. Field Mus. Nat. Hist. Bot. Ser. 16, pts. I and II.