Pacific Science (1999), vol. 53, no. 1: 82–87

Ultraviolet Floral Patterns in the Native Hawaiian Flora: What Do They Mean for Island Biogeography?[1]

C. EUGENE JONES,[2] DEBORAH K. DORSETT,[2] FAITH M. ROELOFS,[3] AND CHIRAG V. SHAH[2]

ABSTRACT: We examined 104 species (13%) of the approximately 784 species of biotically pollinated plants native to Hawai'i and found 14 (13.5%) that have an ultraviolet (UV) floral pattern. However, detailed examination revealed that 32% of the Hawaiian strand species have UV floral patterns, whereas only 8% of the upland species did. All of the flowers with UV patterns measured 1 cm or more in diameter and all but two appear yellow to humans. We discuss several possible explanations for the apparent paucity of UV floral patterns in the native Hawaiian upland flora.

MOST PLANTS HAVE FLOWERS that either completely absorb or very weakly reflect ultraviolet light (UV), and the foliage of most plants is also slightly reflective (Kevan 1983). Many plants are now known to have floral patterns that reflect ultraviolet light and that evidently function to attract and orient pollinating insects (Jones and Buchmann 1974). These patterns of reflection range from being almost completely reflective to possessing a few reflective streaks against an absorptive background.

Earlier investigations, mostly of continental flora, have found that the proportion of species with reflective flowers within a given region varies from about 13% in the Canadian Arctic (Kevan 1974) to as high as 41% of the nonnative species naturalized in the California flora (Guldberg and Atsatt 1974). We examined the flora of the Hawaiian Islands to see if the reflective component of its remote, oceanic island flora would fall within this continental range. Also, Guldberg and Atsatt's analysis of the California flora indicated that certain floral characteristics, such as corolla size and visible color, have a greater propensity to significantly reflect UV. We recorded several floral, taxonomic, and biogeographic characteristics either to determine agreement of the Hawaiian flora with the mainland model or to help establish independent trends.

MATERIALS AND METHODS

From January 1979 to June 1979, native biotically pollinated flowers were collected, taken to the University of Hawai'i at Mānoa, and videotaped using a portable television camera and videotape recorder (Sony model AVC 3400) with a Rodenstock UV-Rodagon F5.6/60 mm UV transmitting lens corrected for wavelengths between 5400 and 3400 Å and fitted with a Tiffen 18A filter (Eisner et al. 1969). In addition, during summer months from 1986 to 1993 flowers were photographed in situ using a 35-mm camera (Canon F1) equipped with a Tiffen 18A UV transmitting filter. Photographs were taken with Kodak Pan X or Plus X film at f 22, and multiple exposures from 5 to 9 sec were made of each flower.

A total of 117 images, of 104 species from 46 families, was made. We noted flowers that reflected UV moderately to strongly, notably distinct from absorptive or lightly reflective backgrounds, and also flowers having distinctive patterns of reflective and absorptive areas. We did not use a gray scale and thus did not attempt to note the percentages of reflectance or reflection coefficients. In addi-

[1] Manuscript accepted 18 March 1998.
[2] Department of Biological Science, California State University, Fullerton, California 92834.
[3] Department of Botany, University of Hawai'i at Mānoa, Honolulu, Hawai'i 96822.

tion, we noted the flower color visible to humans, the corolla diameter, taxonomic affinities, whether the species were native or endemic, woody or herbaceous, and whether the species were strand or upland plants. For the last categorization, we used the definition of strand as discussed in Sohmer and Gustafson (1987) and Whistler (1980): that circumtropical community of plants dispersed onto island shores by ocean currents and affected by shoreline conditions such as salt spray, brackish ground water, and occasional seawater inundation. (This plant community is also referred to as "littoral" but because that term is also used of freshwater lakes, we prefer "strand" to distinguish the seashore community.)

RESULTS AND DISCUSSION

Of 104 species examined, only 14 (13.5%) were found to reflect UV or have a floral pattern of reflectance and absorbency. This is considerably lower than the values reported for most mainland floras and agrees with the value of 13% found in Arctic Canada (Kevan 1974). However, when the species were separated into strand flora and upland flora, an interesting pattern emerged: 32% of the strand species reflected UV, whereas only 7.9% of the upland species did so. Table 1 presents the taxa we sampled with their locations and observed characteristics.

Seven families (15.2% of the 46 sampled families) were found to have some reflective members: Asteraceae, Fabaceae, Goodeniaceae, Malvaceae, Myoporaceae, Sterculiaceae, and Zygophyllaceae. In contrast, of the 61 families sampled by Guldberg and Atsatt (1974) in California, nearly 80% had at least one reflective species.

In corolla size our findings agree with those of Guldberg and Atsatt. They reported that flowers greater than 1 cm in diameter are likelier to reflect UV and that the likelihood of reflectance increases with size. In our study, all but one (*Myoporum sandwicense*) of the reflective flowers were greater than or equal to 1 cm in diameter.

Our results partially disagreed with those of Guldberg and Atsatt concerning the propensity of some visible colors to reflect. Theirs and earlier studies, which they cited, found that yellow and purple flowers were likeliest to reflect UV and that white and green flowers usually did not. Eleven of the 14 reflective Hawaiian flowers were yellow and none of the green flowers sampled reflected UV, but the other three reflective flowers were white. Hawai'i has relatively few species with purple or violet flowers and none that we sampled reflected UV.

We consider our sample size to be quite robust. There are approximately 980 species of angiosperms in Hawai'i (Sohmer 1994) and about 20% of these are wind-pollinated (Carlquist 1974), leaving 784 biotically pollinated species. Our sample of 104 species represents 13.3% of the biotically pollinated species and 10.6% of the total angiosperms. In contrast, Guldberg and Atsatt (1974) sampled 300 species of California plants, but this represents only about 5% of the approximately 5700 species of angiosperms there (Hickman 1993). We are confident, therefore, that our survey presents an accurate picture of UV floral reflectance in Hawai'i.

What can account for Hawai'i's apparent dearth of UV-reflecting flowers? There are two probable explanations: either few reflective species successfully colonized the Hawaiian Islands or a number of reflective species did establish but subsequently lost this ability. Each of these explanations presents dilemmas. In the case of failure to colonize, why should UV reflectance limit the ability of a species to disperse or establish new populations? In the second case, what factors present in Hawai'i could select against flowers reflecting UV?

There are several avenues of investigation that need to be explored. An examination of the nonreflective species' closest relatives or the mainland populations from which the colonists originated might yield clues. Does Hawai'i's pattern hold true on other oceanic islands? Do continental islands also follow this pattern or are their species more likely to resemble those on the mainland? Because UV reflective patterns are known to be of importance in plant-pollinator interactions, what

TABLE 1

SPECIES INVESTIGATED FOR ULTRAVIOLET FLORAL PATTERNS

SPECIES	SITE[1]	VISIBLE COLOR	UV[2]	SIZE[3]	HABIT	HABITAT
Aizoaceae						
Sesuvium portulacastrum	SB	Violet pink	0	<	Herb	Strand
Amaranthaceae						
Charpentiera elliptica[4]	LA	Whitish, reddish (2 plants)	0	<	Woody	Upland
Nototrichium sandwicense	LA	Whitish	0	<	Herb	Upland
Apocynaceae						
Alyzia oliviformis	MC	Greenish cream	0	<	Woody	Upland
Rauvolfia sandwicensis	LA	Whitish	0	<	Woody	Upland
Aquifoliaceae						
Ilex anomala	MK	White	0	≤	Woody	Upland
Araliaceae						
Tetraplasandra sp.[5]	LA	Green, reddish anthers	0	≥	Woody	Upland
Arecaceae						
Prichardia arecina	UH	Whitish	0	<	Woody	Upland
Pritchardia affinis	Hawai'i	White	0	<	Woody	Upland
Asteraceae						
Argyroxiphium sandwicense	Maui	Red	0	>	Woody	Upland
Bidens menziesii	Maui	Yellow	+	>	Woody	Upland
Bidens molokaiensis	DH	Yellow	+	>	Herb	Upland
Bidens sp	MC	Yellow	+	>	Herb	Upland
Bidens sp.	WN	Yellow	+	>	Herb	Upland
Dubautia knudsenii	AT	Reddish	0	>	Woody	Upland
Dubautia menziesii	Maui	Yellow	0	≥	Woody	Upland
Lipochaeta integrifolia	SB	Yellow	+	>	Herb	Strand
Lipochaeta lobata	SB	Yellow	+	>	Herb	Strand
Remya mauiensis	Maui	White	0	≤	Woody	Upland
Tetramolopium consanguineum	Hawai'i	White	0	<	Woody	Upland
Boraginaceae						
Heliotropium anomalum	SB	White	0	≤	Woody	Strand
Campanulaceae						
Brighamia insignis	Maui	White	0	>	Herb	Upland
Clermontia clermontioides	Kaua'i	White	0	>	Woody	Upland
Clermontia kakeama	O'ahu	Green	0	>	Woody	Upland
Clermontia oblongifolia	MC	Green	0	>	Woody	Upland
Clermontia persicifolia	WN	White	0	>	Woody	Upland
Cyanea superba	O'ahu	White	0	>	Woody	Upland
Rollandia lanceolata	O'ahu	Purple	0	>	Woody	Upland
Trematolobelia macrostachys	MK	Pink	0	>	Woody	Upland
Caryophyllaceae						
Schiedea globosa	Maui	Green	0	<	Herb	Strand
Convolvulaceae						
Ipomea littoralis	O'ahu	Purple	0	>	Herb	Strand
Ipomoea pes-caprae	SB	Violet	0	>	Herb	Strand
Jacquemontia ovalifolia	SJ	Light blue	0	>	Herb	Strand
Ebenaceae						
Diospyros hillebrandii	WN	Whitish green	0	≤	Woody	Upland
Diospyros sandwicensis	Maui	Red	0	<	Woody	Upland
Elaeocarpaceae						
Elaeocarpus bifidus	MC	Green–cream	0	≤	Woody	Upland
Epacrideaceae						
Styphelia tameiameiae	MK	Whitish	0	<	Woody	Upland
Ericaceae						
Vaccinium calycinum	Maui	Greenish	0	<	Woody	Upland

TABLE 1 (continued)

SPECIES	SITE[1]	VISIBLE COLOR	UV[2]	SIZE[3]	HABIT	HABITAT
Euphorbiaceae[5]						
Chamaesyce celastroides	SJ	Greenish white	0	<	Woody	Strand
Chamaesyce degeneri	SB	Greenish	0	<	Herb	Strand
Chamaesyce multiformis	MC	Greenish	0	<	Woody	Upland
Claoxylon sandwicense	AT	Greenish, white anthers	0	<	Woody	Upland
Fabaceae						
Acacia koa	MV	Light yellow	0	≤	Woody	Upland
Canavalia galeata	WN	Violet purple	0	>	Woody	Upland
Canavalia pubescens	Maui	Red	0	>		Upland
Erythrina sandwicensis	Maui	Red	0	>	Woody	Upland
Sesbania tomentosa	WA	Reddish	0	>	Herb	Strand
Sophora chrysophylla	Maui	Yellow	0	>	Woody	Upland
Vigna marina	O'ahu	Yellow	+	>	Herb	Strand
Gesneriaceae						
Cyrtandea gayana	AT	White	0	>	Woody	Upland
Cyrtandra grandiflora	MC	White	0	>	Woody	Upland
Cyrtandra sandwicensis	MC	White	0	<	Woody	Upland
Goodeniaceae						
Scaevola coriacea	SJ	White inside, purple/green outside	0	>	Woody	Strand
Scaevola gaudichaudiana	MC	White	+	>	Woody	Upland
Scaevola mollis	LA	White, center and veins purple	0	>	Woody	Upland
S. mollis x S. gaudichaudiana[6]	WN	White, purple near throat	0	>	Woody	Upland
Scaevola sericea	SB	Whitish with yellow throat	0	>	Woody	Strand
Gunneraceae						
Gunnera petaloidea	MK	Greenish, anthers red	0	<	Woody	Upland
Hydrangeaceae						
Broussaisia arguta	MK	Pinkish	0	<	Woody	Upland
Lamiaceae						
Lepechinia hastata	WA	Red purple	0	≥	Herb	Upland
Liliaceae						
Dianella sandwicensis	WN	White	0	≥	Herb	Upland
Malvaceae						
Abutilon menziesii	Lāna'i	Reddish pink	0	>	Woody	Upland
Gossypium tomentosum	SJ	Yellow	0	>	Woody	Strand
Hibiscadelphus distans	Kaua'i	Green	0	>	Woody	Upland
Hibiscus arnottianus	MC	White, central column red purple	+	>	Woody	Upland
Hibiscus brackenridgei	WA	Yellow	0	>	Woody	Upland
Hibiscus calyphyllus	LA	Yellow, throat purple	0	>	Woody	Upland
Hibiscus kokio	NT	Reddish	0	>	Woody	Upland
Hibiscus tilliaceus	O'ahu	Yellow	+	>	Woody	Strand
Kokia cookei	O'ahu	Red	0	>	Woody	Upland
Sida sp.	WN	Orange	0	>	Herb	Upland
Sida fallax	SJ	Yellow orange	+	>	Herb	Strand
Menispermaceae						
Cocculus trilobus	WN	Whitish	0	<	Woody	Upland
Myoporaceae						
Myoporum sandwicense	SB	White	+	≤	Woody	Strand
Myrsinaceae						
Myrsine alyxifolia	AT	Whitish	0	<	Woody	Upland
Myrtaceae						
Metrosideros polymorpha[4]	MC, WN	Red, yellow (2 plants)	0	>	Woody	Upland
Nyctaginaceae						
Boerhavia glabrata	Maui	White	0	>	Herb	Strand
Boerhavia repens	SB	Pinkish	0	<	Herb	Strand
Pisonia umbellifera	MC	Pinkish	0	<	Woody	Upland
Papaveraceae						
Argemone glauca	KH	White	0	≤	Herb	Upland

TABLE 1 (continued)

SPECIES	SITE[1]	VISIBLE COLOR	UV[2]	SIZE[3]	HABIT	HABITAT
Piperaceae						
Peperomia menbranacea	WN	Greenish	0	<	Herb	Upland
Pittosporaceae						
Pittosporum sp.	LA	White	0	>	Woody	Upland
Plumbaginaceae						
Plumbago zeylandica	EO	White	0	≥	Herb	Strand
Portulaceae						
Portulaca lutea	Maui	Yellow	0	>	Herb	Strand
Rhamnaceae						
Alphitonia ponderosa	Kaua'i	White	0	<	Woody	Upland
Rubiaceae						
Bobea elatior	WN	Whitish green	0	<	Woody	Upland
Coprosma ochracea	MK	Greenish white	0	<	Woody	Upland
Hedyotis centranthoides	MK	Greenish, tube purple	0	≤	Woody	Upland
Hedyotis terminalis	MC	Green	0	≤	Woody	Upland
Psychotria grandiflora	AT	White	0	≤	Woody	Upland
Psychotria hexandra	MC	White	0	≥	Woody	Upland
Psychotria sp.	WN	Whitish	0	≥	Woody	Upland
Rutaceae						
Pelea clusiifolia	WN	Whitish	0	≤	Woody	Upland
Santalaceae						
Santalum ellipticum	EO	Greenish white, aging red purple	0	<	Woody	Upland
Santalum freycinetianum	WN	Whitish inside, reddish outside	0	≤	Woody	Upland
Sapotaceae						
Pouteria sandwicensis	MC	Greenish white	0	<	Woody	Upland
Sterculiaceae						
Waltheria indica	SB	Yellow	+	≥	Herb	Strand
Thymeliaceae						
Wilkstromia sp.	WN	Green flowers, orange anthers	0	<	Woody	Upland
Urticaceae						
Neraudia melastomaefolia	WA	Greenish with white anthers	0	≤	Woody	Upland
Pipturus albidus	MC	Greenish	0	<	Woody	Upland
Verbenaceae						
Vitex rotundifolia	SB	Purple	0	≥	Woody	Strand
Violaceae						
Viola chamissoniana	WC	White	0	>	Woody	Upland
Viscaceae						
Korthalsella complanata	WN	Yellowish green	0	<	Woody	Upland
Zygophyllaceae						
Tribulus cistoides	DH	Yellow	+	>	Herb	Strand

[1] Site refers to location where plant was collected or photographed: AT, Awa'awapuhi Trail, Kōke'e, Kaua'i; EO, 'Ewa, O'ahu; HM, Haleakalā, Maui; KH, Kona, Hawai'i; LA, Lyon Arboretum, O'ahu; MC, Mānoa Cliffs Trail, O'ahu; MK, Mt. Ka'ala, O'ahu; MV, Moanalua Valley, O'ahu; NT, National Tropical Botanic Garden, Kaua'i; SB, Sandy Beach, O'ahu; SJ, St. John Courtyard, O'ahu; UH, University of Hawai'i, Mānoa; WA, Waimea Arboretum, O'ahu; WC, Waimea Canyon, Kaua'i; WN, Wai'alae Nui, O'ahu; DH, Diamond Head, O'ahu; no acronym indicates an undisclosed location on that island.

[2] 0, flower entirely absorptive; +, a UV-reflective pattern was seen.

[3] Refers to flower width greater than, less than, or equal to 1 cm in diameter.

[4] Two flower color morphs. Separate images taken of each color.

[5] Apetalous; visible color refers to sepals or bracts.

[6] Natural hybrid.

role might Hawai'i's pollinating insect fauna have played in reducing the number of species that reflect UV? Do the native Hawaiian pollinating insects have the ability to detect UV? Many of Hawai'i's flowers are pollinated by moths or butterflies. Many lepidopterans detect and respond to UV patterns on their wings (Silberglied and Taylor 1978), but it is not known whether UV patterns are important floral cues for them. Also, although

Hawai'i has more than 60 native species of bees, all of them are members of a single genus, *Hylaeus*, in the family Colletidae, subfamily Hylaeinae (Howarth and Mull 1992). This family, with many similarities to sphecoid wasps, is generally regarded as the most primitive of the bees (Michener 1944), and these bees may not detect or respond to UV as the more advanced families do. Clearly, studies are needed on the plant-animal interactions involving both the reflective and nonreflective species.

ACKNOWLEDGMENTS

We acknowledge the cooperation and assistance received from the Botany Department at the University of Hawai'i at Mānoa and particularly the assistance of Gerald Carr and Coleen Cory.

LITERATURE CITED

CARLQUIST, S. J. 1974. Island biology. Columbia University Press, New York.

EISNER, T., R. E. SILBERGLIED, D. ANESHANSLEY, J. E. CARREL, and N. H. HOWLAND. 1969. Ultraviolet video-viewing: The television camera as insect eye. Science 166:1172–1174.

GULDBERG, L. D., and P. R. ATSATT. 1974. Frequency of reflection and absorption of ultraviolet light in flowering plants. Am. Midl. Nat. 93(1): 35–43.

HICKMAN, J. C., ED. 1993. The Jepson manual: Higher plants of California, Appendix 1: Floristic summary. University of California Press, Berkeley.

HOWARTH, F. G., and W. P. MULL. 1992. Hawaiian insects and their kin. University of Hawai'i Press, Honolulu.

JONES, C. E., and S. L. BUCHMANN. 1974. Ultraviolet floral patterns as functional orientation cues in hymenopterous pollination systems. Anim. Behav. 22:481–485.

KEVAN, P. G. 1974. Floral colors in the high arctic with reference to insect-flower relations and pollination. Can. J. Bot. 50: 2289–2316.

———. 1983. Floral colors through the insect eye: What they are and what they mean. Pages 3–30 *in* C. E. Jones and R. J. Little, eds. Handbook of experimental pollination biology. Van Nostrand Reinhold, New York.

MICHENER, C. D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bull. Am. Mus. Nat. Hist. 82:151–326.

SILBERGLIED, R. E., and O. R. TAYLOR. 1978. Ultraviolet reflection and its behavioral role in the courtship of the sulphur butterflies *Colias eurytheme* and *C. philodice* (Lepidoptera, Pieridae). Behav. Ecol. Sociobiol. 3:203–243.

SOHMER, S. H. 1994. Conservation and the manual of flowering plants of Hawai'i: A sense of reality. Pages 43–51 *in* C. I. Peng and C. H. Chou, eds. Biodiversity and terrestrial ecosystems. Academia Sinica Monograph Series No. 14. Institute of Botany, Taipei.

SOHMER, S. H., and R. GUSTAFSON. 1987. Plants and flowers of Hawai'i. University of Hawai'i Press, Honolulu.

WHISTLER, W. A. 1980. Coastal flowers of the tropical Pacific. Oriental Publishing Co., Honolulu.