https://doi.org/10.1051/e3sconf/202343403004

Study on the frequency of ultraviolet (UV) light reflectance and absorption in native and nonnative flowering plants

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Abstract. In addition to the floral shape and colors seen by the human eye, ultraviolet (UV) reflectance serves as a significant visual advertisement for pollinators of many blooming plant species. The interaction between flowers and pollinators is significantly influenced by plant UV patterns. It is common knowledge that many flowers have vacuolated pigments that are UV-absorbing in their petal cells. Nevertheless, the impact of UV reflection and absorption on pollinators to particular plant species hasn't been properly investigated. In this paper, the degree and pattern of UV light reflection in flowers of 240 plant species from 55 families were examined. Four levels of UV absorption and reflection were used to rank the flowers. While white and green flowers often reflect UV weakly, yellow and violet flowers have the highest likelihood of doing so. In general, pollination aids were nonreflective and independent of hue. UV reflection seems to be positively connected with flower size even though it is unrelated to floral symmetry. UV reflection is certainly present in all plant families; however, it seems to be more prevalent in some taxonomic groups. UV reflection and absorption appear to be influenced by the physical features and chemical make-up of the petals, just like other floral petals.

1. Introduction

The coevolution of flowers and pollinating insects has produced a variety of specific recognition signals which increase pollinator efficiency. The interactions between entomophilous flowers and the insects that pollinate them have developed through coevolution. These connections are made possible by one or more flower attributes (such as pollen, nectar, odor, and visual phenomena). In addition to the flower's size and shape, pollinators are attracted to flowers by their color(s) and contrast with their surroundings. Many flowers have patterns of contrasting color (nectar guides), which might be in the shape of concentric circles, lines that extend outward from the center, or color blotches. Flower size, shape, scent, color and pattern often correspond to morphological and sensory characteristics of the pollinator [1]. Floral markings of contrasting colors cue visiting insects to the location of food and have long been known as nectar guides [2, 3, 4]. Many such guides consist of patterns of differential ultraviolet (UV) reflection making them visible to most pollinating insects but invisible to man. Although extracts of floral petals were noted to reflect UV as early as 1872 (Kraus), UV was not fully accepted as an important component of floral coloration until relatively recently. Due of these differences in UV coloration from other plants in the area, UV vision facilitates floral visitors in identifying the particular flowers of these plants. Some flowers produce a contrasting pattern of UV absorbance and reflectance on the surface of their petals to promote distinction by specific kinds of pollinators, while others contrast

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petals and reproductive organs by an inverse pattern of UV absorbance and reflectance. Several early researchers used still photography with special quartz lenses to survey flowers for reflection of UV [5]. The most meaningful survey of floral coloration to date was accomplished by Daumer (1958) [6], again using complicated laboratory techniques geared to the trichromatic color system of the honeybee. Based on simple additive mixing of colors, his work provided a discerning interpretation of how flowers present themselves to potential insect visitors. In 1969, Eisner et al., pointed out the intrinsic sensitivity of the television camera to UV and demonstrated its value in directly observing and recording UV reflection and adsorption [7].

This study describes the association between UV reflection and flower color, pattern, size, form and taxonomic category in 240 plant species representing 55 angiosperm families. We survey only one component of floral coloration and do not attempt to define how flowers actually appear to their pollinators. The physical and chemical basis for patterns of UV reflection are also briefly considered.

2. Methods

The floral UV patterns of 240 plant species were determined with the aid of s Sony model AV-3400 field-pack videorecorder equipped with a Zeiss-Jena 60 mm/f-4 quartz lens and Zeiss UG2 visible light filter. All observations were made in the field during the spring of 2021 using full sunlight as a source of UV energy. Kodak Tri-X panchromatic film and a Kodak 18A visible light filter were used for still UV photography.

A UV-gradient standard was constructed by dividing a circular Sears paint chip into for sections. Section 1 and 2 were covered with a heavy and thin coat, respectively, of Testors brand silver metallic paint, producing 2 deg of UV reflection, strong and moderate. Sections 3 and 4 represented two categories of UV absorption. Section 3 was unmodified and absorbed UV moderately while section 4 was coated with flat black paint and absorbed UV strongly (Figure 1). The standard was attached to a rod projecting 1 m in front of the camera lens. Flowers were hand-held next to the standard and scored (1-4) for their reflection-absorption intensity and pattern. Additional data taken for each species included flower color, nectar guide color, symmetry, floral diameter (at aperture) family and genus and species when known. Our sample consisted of 183 species native to Tashkent region and 117 nonnative species. The nonnative species were observed in several botanic gardens, with the exception of 20 naturalized Tashkent species which we chose to include in the latter category.

3. Results and Discussion

Earlier investigations suggest that approximately one-third of all flowers significantly reflect near UV [8, 9]. The frequency of reflection value for our total sample agrees closely with this figure (Table 1). Although chi-square tests indicate neither the native nor nonnative portion of our sample differs significantly from this previously reported frequency of 33%, use of the *z* statistics suggests that the proportion of reflective flowers is significantly higher among nonnative species. Eleven of our sample of 15 naturalized Tashkent species reflect UV. It would be interesting to compare the relative UV reflection of pollinator-dependent naturalized and native species that grow and flower together, the implication being that bright UV reflection may be of greater significance in pollinator competition to colonizing migrants than to native species.

Similar frequencies of reflection between the actinomorphic and zygomorphic flowers (Table 1) suggest that UV reflection is independent of basic floral symmetry. The frequency of reflection becomes greater with increasing flower size (diameter at aperture) (Table 1). This is due in large part to flowers with moderate reflection, where probability of reflection increases with size, and to strongly absorbing flowers where the opposite trend occurs. Strong reflectance and moderate absorption remain relatively constant in all flowers over 1 cm in diam. A possible source of error exists in categorizing reflection in the smallest flowers, simply because of the paucity of clearly observable surface area and the high degree of light diffusion caused by the inflorescences into which small flowers are often arranged. One explanation for the low probability of reflection in small flowers is that these may more often be autogamous and less dependent upon cross-pollination. Tests of this possibility were not attempted due to the difficulty of assessing the breeding system of each species.

Earlier surveys have made no specific references to tendencies for reflection of absorption within taxa above the species level. The wide range of frequency values among our family samples suggests that measurable consistencies might exist on a family or genus level (Table 2). Families – at least moderately well sampled – which seem to have a low probability of reflecting, are the Ericaceae, Labiatae and Polemoniaceae, while the Amaryllidaceae, Geraniaceae, Leguminosae and Renunculaceae often reflect. These figures are, of course, simply suggestions for more careful examination of these groups.

Table 1. Ultraviolet reflection/absorption characteristics according to sample origin, floral symmetry and size (the percentage of strongly and moderately reflecting species were summed to give a "frequency of reflection" for each category)

Floral characteristics	Sample size	Reflection		Total, inch	Absorption	
		Strong, inch	Moderate, inch		Moderate, inch	Strong, inch
Origin:						
Tash. natives	183	0.13	0.14	0.27	0.50	0.23
Nonnatives	117	0.20	0.21	0.41	0.53	0.06
Total sample	300	0.16	0.17	0.33	0.51	0.16
Symmetry						
Actinomorphic	215	0.16	0.15	0.31	0.51	0.18
Zygomorphic	85	0.16	0.20	0.36	0.51	0.12
Size (diam in cm)						
0.0-0.9	81	0.06	0.09	0.15	0.62	0.23
1.0-2.4	125	0.20	0.15	0.35	0.48	0.17
2.5-4.9	69	0.19	0.20	0.39	0.48	0.13
5.0-7.4	15	0.20	0.33	0.53	0.47	0.00
7.5	10	0.20	0.50	0.70	0.30	0.00

Approximately 7% of the total sample possessed patterns normally unseen in visible light, formed by differential reflection of UV wavelengths. Seventeen of 22 flowers exhibiting such patterns appear yellow in the visible spectrum. Thompson et al. (1972) [12] point out that flavanols, which they consider to be the major chemical factor responsible for UV absorbing patterns, also appear yellow in the visible spectrum. These patterns invariably consisted of dark central regions of various shapes surrounded by a brightly reflecting background. Some common native species with invisible nectar guides include *Amsinckia menzeisii, Angallis arvensis, Brassica campestris, Collinsia heterophyla, Erodium botrys, E. cicutarium, E. moschatum, Hypochoeris glabra, Mimulus guttatus, Ranunculus arvenis, Sisymbrium irio, S. orientale* and *Taraxacum officinale*. Bees encountering central UV absorbing areas exhibit an instinctive response of lowering the head and proboscis toward the petal surface, demonstrating the effectiveness of such patterns as pollination guides [13, 14, 15].

Table 2. Frequency of reflection by family (families at least moderately sampled and which appear to exhibit consistencies in terms of UV reflection are marked with an asterisk)

Family	Frequency of reflection	Sample size (inch)	Family	Frequency of reflection	Sample size (inch)
Acanthacecae	0.67	3	Onagraceae	0.47	15
Amaryllidaceae	0.55	9	Orchidaceae	0.36	14
Berberidaceae	0.33	3	Oxalidaceae	0.33	3
Boraginaceae	0.40	5	Papaveraceae	0.17	6
Caryophyllaceae	0.25	4	Pittosporaceae	0.00	2
Compositae	0.38	37	Polemoniaceae	0.08	12
Crassullaceae	0.00	2	Polygonaceae	0.00	4
Cruciferae	0.31	16	Primulacecae	0.50	2
Ericaceae	0.00	5	Ranunculaceae	0.50	8
Euphorbiaceae	0.50	2	Rhamnaceae	0.00	4
Geraniaceae	0.86	7	Rosaceae	0.25	8
Hydrophyllaceae	0.33	6	Saxifragaceae	0.22	9
Iridaceae	0.67	3	Scrophulariaceae	0.38	21
Labiatae	0.08	12	Solanaceae	0.50	4
Leguminosae	0.54	24	Umbelliferae	0.00	4
Liliaceae	0.60	5	Violaceae	0.50	2
Malvaceae	0.44	9	Miscellaneous	0.41	27
Myrtaceae	0.00	3			

Frequency of UV reflection among categories of basic visible petal colors is shown in Figure 1. In arrangement with previously reports findings, yellow and violet flowers exhibited a particularly high probability of reflecting, while white and green flowers generally did not reflect UV [10, 11]. Pollination guides usually absorbed UV regardless of their visible color. The exception to this generalization seems to be white nectar guides, of which 31% significantly reflect UV. The high-frequency value for red markings (Table 2) may be the result of small size (seven). Exposed stamens and pistils were often involved in the formation of patterns of UV reflection.

Increasing appreciation of the importance of UV reflection has resulted in the current use of this character in several areas of floral biology research [16]. However, generalizations concerning the biological significance of floral UV patterns will have to await the syntheses of detailed studies of many specific pollinator-UV relationships. Knowledge of the visual sensory system of pollinators must precede interpretations of how a particular flower is visually experienced by that organism. Daumer's careful work with honeybees defines no fewer than 10 differentiable "bee colors" based on different combinations of yellow, blue-green, blue and UV wavelengths. A constant amount of UV may have different effects when combined with light of various wavelengths [17]. For example, a mixture of 50% UV and 50% blue light is experienced by honeybees as a unique "bee-violet". When mixed with longer wavelength yellow light in the same proportion, however, the UV dominates the mixture so that it is seen by bees as pure UV. This kind of data combined with new information on the nature of UV pigments, may give us considerable insight about the selective value of certain visible colors.

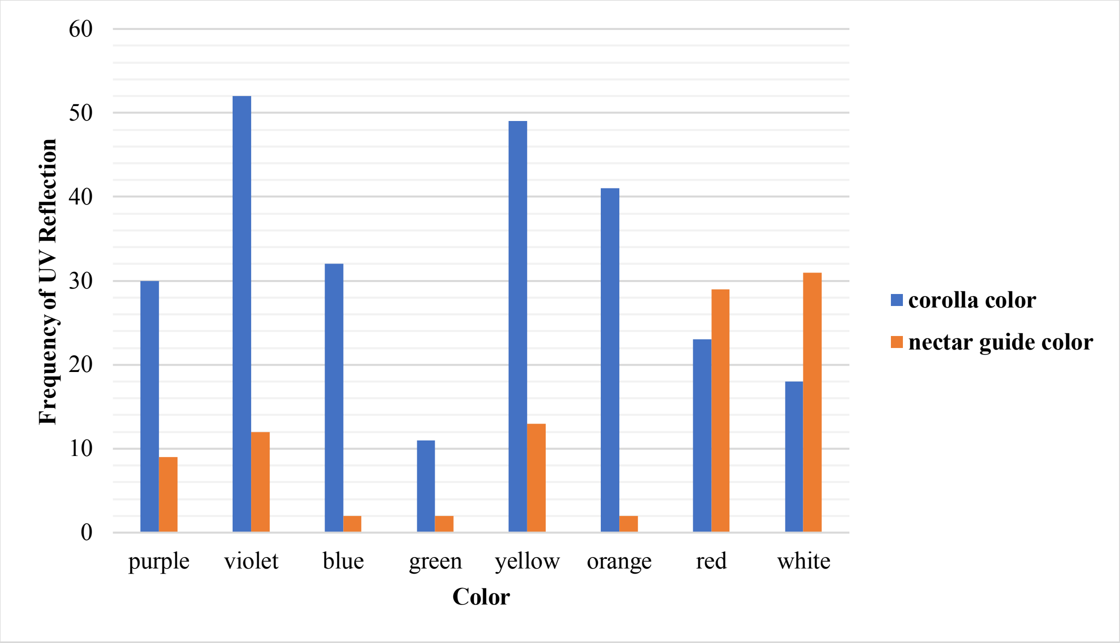

Fig. 1. Frequencies of UV reflection for several visible floral colors

Until more is known about the physical and chemical basis of UV reflection and absorption, we can only speculate about the genetic difficulty of acquiring a particular state of the trait, and the energetic costs of its maintenance. The recent studies show that UV absorption in the petals of *Rubeckia hirta* is due to the presence of flavanols are of widespread occurrence in flowers [12]. Researchers suggest that the primary adaptive function of these pigments is UV absorption.

The basis for floral UV reflection has not yet been clearly defined, but like other floral coloration, control of UV seems to involve both physical and chemical characteristics of petal tissues. Flowers owe their visible color to unique combinations of chlorophylls, carotenoids, xanthophylls, flavonoids, anthocyanins and anthoxanthins distributed in different ways in the petal tissues [18, 19, 20]. Given the chemical basis for reflection of visible wavelength, and for the absorption of UV, one would predict that bright UV pattern is also due to the presence of one or more reflecting pigments. Some circumstantial evidence suggests this will prove to be true. The data of Thomphson et al. [11] show a dip at 360 nm in the absorption spectrum of the methanolic extract of the brightly reflecting petal tips of *Rudbeckia* *hirta*. By observing petals before and after extraction with methanol, we noted several brightly reflecting species which exhibited a marked decrease in reflection as a result of the extraction. The possibility of tissue damage during the extraction cannot be discontinued as a possible explanation for the decreased UV reflection, but it is not the most probable explanation. By spotting the methanolic extract of the brightly reflecting petal tips of *Taraxacum officinale* on nonreflective petals, we were able to reproduce a level of reflection equal to that of the original *Taraxacum* petals. This demonstration obviously suffers from the fact that physical surface characgteristics are altered by applying the extract. We can only note that our extract, like that of *Rudbeckia*, showed a pronounced dip in the absorption spectrum between 360 and 380 nm, suggesting the presence of a reflecting pigment. We have also observed that UV reflection undergoes developmental alterations independently of visible pigmentation in *Encelia farinose*.

4. Conclusions

Thus, there is conclusion that bright reflection results simply from the lack of UV absorbing compounds in the epidermis.

More than half of the species in our survey exhibit neither pronounced UV reflection nor absorption (Table 1, category 3). This disproportionately high frequency of UV "neutrality" may be due to the energetic costs of maintaining strongly reflecting or absorbing pigments, restricting their distribution to situations where the character is of pronounced selective value. Future work on the biological significance of floral UV should give equal consideration to both reflection and absorption, particularly to flowers that are totally and strongly absorbent. Our sample shows that this UV category is being maintained at a frequency equal that of bright reflection; yet its significance is obscure. One could argue that bird-pollinated flowers gain better protection against insect predators by being both red and darkly UV absorbing, but our data suggest that the frequency of this trait remains relatively constant over all major flower colors. Correlation of the character with plant habitat, breeding system and pollinator sensory stimuli and temporal activity should provide interesting data complimentary to studies of UV reflection.

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