ULTRAVIOLET COMPONENTS OF FLOWER

COLOR IN A BOG HABITAT

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A   VISIBLE

B   UV
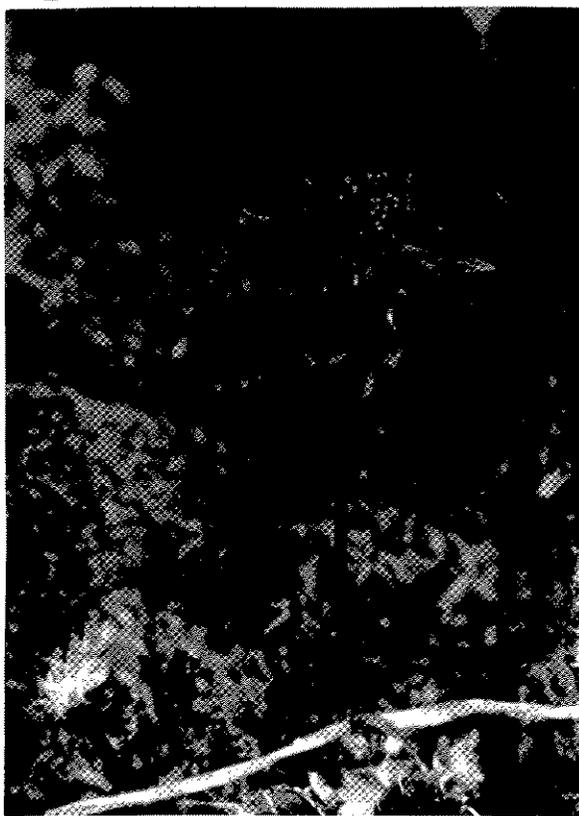
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Introduction

Floral coloration is an important component of pollinator attraction: among entomophilous flowers, reflectance of wavelengths in both the "visible" spectrum (400-700 mμ) and in the near ultraviolet (300-400 mμ) contribute to color patterns. Studies in insect color vision have concluded that many groups have behavioural or physiological responses to ultraviolet light (for review see Burkhardt 1962, Goldsmith and Bernard 1974). In addition, for several species tested, acuity and wavelength discrimination were greatest in UV (Daumer 1958).

Few flowers show overall UV reflectance, but floral patterns created by contrasting reflectance qualities are common (Silberglied 1979). UV patterns may promote insect-mediated pollination by signalling availability of food rewards (Frolich 1976), eliciting feeding behaviour (Daumer 1958), orienting insects to nectaries (Jones and Buchmann 1974), or distinguishing morphologically similar species (Horovitz and Cohen 1972).

Analysis of inter-floral UV reflectance has often taken

precedence over examination of the photic regime in the natural habitats of flowering plants, and of the backgrounds against which pollinators might perceive flowers. Frolich (1976) demonstrated that UV contrast patterning extended to the buds, leaves and substrate of the inflorescence, and that generalizations on the UV reflectance of backgrounds may not always be valid.

The present study examines UV reflectance among 12 species of flowering plants found in the Sphagnum bog habitat. It describes floral backgrounds and patterning within flowers, in an attempt to define the micro-habitats in which insects might perceive them. Since UV acts in concert with reflectance of wavelengths greater than 400 mμ, coloration of flowers and backgrounds in the visible spectrum is referred to as well.

Methods

Floral reflectance in longwave ultraviolet (350-400 mμ) was assessed by photographing each species through a UV-transmitting filter (Kodak 18A) mounted on a Canon Macro lens and AT-1 body. A comparison in unfiltered light (400-700 mμ) accompanied each UV photograph. Tri-ex 400 ASA was shot at

f/11 for maximum depth of field. Comparative UV reflectance
was determined by including a 4-point graded reflectance scale
in each UV frame. Floral reflectance in the human spectrum
was assessed visually, but where colors were difficult to
name (for example, in the red-pink complex), species were
photographed through a series of 5 filter combinations that
isolated wavebands across the visible spectrum. Outdoor
sunlight was used for illumination in all cases.

Each species was photographed in its habitat close enough
to show details of the flower and its immediate background,
and from 1 to 3 m away. Photographs were taken at the angle
which revealed the greatest diameter of the corollas; for
aggregate flowers, this involved frames at several angles.

Measurements were made of corolla size, aggregate flower
cluster size (where applicable), plant height, and the distance
from the corolla to its background. Background plants and soils
and their coloration were documented. Numbers of open corollas
in meter quadrants were recorded for each species at peak
flowering.

Insect pollinators were collected and identified. Anec-
dotal records were kept on pollinator movement, of hovering,

flying and approach to flowers, and of feeding behaviour.

Results

UV reflection within flowers

Of the 12 species examined under spectrophotometry, 8 showed petals that strongly absorbed UV light, 2 showed moderate reflectance and 2 strong UV reflectance (Table 1, Figure 1). All species expressed UV detail that contrasted with the reflectance of the petals and primarily emphasized pollen or nectar bearing flower parts.

In Rubus chamaemorus, Coptis trifolia and Vaccinium oxycoccus, anthers reflected UV; in Kalmia polifolia and Tofieldia glutinosa, nectaries were reflectors, and in Trientalis europaea, Gentiana douglasiana and Ledum palustre ssp. groenlandicum, both pollen and nectar were UV-reflecting. The central portion of flowers (all species were radially symmetrical) was emphasized in UV by reflectant stigmas in K. polifolia, T. europaea and Loiseleuria procumbens. Filaments contrasted

with absorbant petals by reflecting UV (T. europaea and
L. palustre) or with moderately reflectant petals by
strong UV absorption (K. polifolia and R. chamaemorus).
The central third of Apargidium boreale was strongly
absorbant while the outer whorl of florets reflected UV
light; pistils appeared as radiating lines against the outer
florets by strong absorption. Fauria crista-galli as well,
showed concentric contrasting whorls, with radiating lines
on the petals.

UV-absorbing corollas appeared white in the visible
spectrum in 5 of the species and violet/red in the remaining
3. The 4 flowers with greater reflectance in UV were, in
visible light, 1 violet/red, 2 white and 1 yellow. The UV
patterns were often synonomous with distinctions in other
wavelengths. In G. douglasiana, yellow nectaries and a
semi-circle of yellow spots around them reflect in UV,
as do the deep violet anthers. Anthers in T. europaea,
R. chamaemorus, V. oxycoccus

and L. palustre were emphasized by contrast in both visible and UV light, as were the nectaries and stigma in K. polifolia, the pistil in C. trifolia, and the stigma in L. procumbens. In several cases, UV reflection formed patterns not evident in visible wavelengths, such as the "bull's eye" and radiating lines of A. boreale and F. crista-galli, UV-reflecting nectar in K. polifolia, T. glutinosa, T. europaea and L. palustre, and strong differentiation of anthers in C. trifolia and stamens in T. europaea.

In summary, UV absorbance was proportionately greater than UV reflectance in 8 of the 12 species studied. UV patterning in all flowers accentuated the reproductive parts and was often coincident with distinctions in visible wavelengths. Generally, these patterns revealed concentric bands of alternating reflectance and absorbance, sometimes with "speckling" in central portions and radiating lines.

Growth habits

The effect of overall floral colors in the field will involve the density of corollas, their size, orientation, and height above the substrate. There were two main growth modes among

(Table 2)
bog flowers that were differentiated as well in UV reflectance
patterns. Species with small corollas (<15 mm) showed a
high corolla density during peak flowering (10-31/m²),
while those with larger corollas (>20 mm) were solitary or
partially clustered (<4/m²). Small-flowered species had
UV-absorbing petals, and larger-flowered were moderately to
highly reflectant.

Trends in growth habits associated with reflectance in
visible wavelengths was not evident. Among clustered, small-
flowered species, 5 were white and 3 violet/red; low density,
large-flowered species included 2 white, 1 yellow and 1 violet/
red.

The orientation of the corolla will contribute to its
visibility to pollinators: for species with spreading petals,
there appears to be an optimal angle at which floral coloration
and morphological cues will be best revealed to pollinators. For
urceolate, reflexed or aggregate flowers, the visibility of the
inflorescence would be similar from many angles.

Five of the 7 species that lie close to the substrate
(<10 cm tall) had spreading petals that oriented horizontally
(G. douglasiana , C. trifolia, T. europaea, L. procumbens,

R. chamaemorus); in the other two (A. polifolia, V. oxycoccus), although effective orientation of corollas is difficult to determine, the radially symmetrical plane of each corolla type (urceolate and reflexed respectively) is oriented to the horizontal. All of these except R. chamaemorus have UV-absorbing petals. T. glutinosa and L. palustre, which absorb UV as well, were tall (>15 cm) and had various corolla orientations among each aggregate flower cluster. Species that reflected more strongly in UV (K. polifolia, A. boreale, F. crista-galli) were tall (>15 cm) with corollas oriented vertically.

On the bog, insect pollinators were observed flying at heights of less than 0.5 m: corollas which were over 15 cm above the substrate oriented vertically, or had a large proportion of the aggregate corollas orienting vertically, having the effect of maximizing the visual impact of the flower on approaching pollinators. Conversely, those flowers which lay close to the substrate oriented horizontally and would be maximally visible from above. None of the species were heliotropic.

UV reflectance qualities of the bog habitat

The bog habitat is open to all wavelengths of light.
Although only 3% of light reaching the ground is shorter
than 400 mμ (Silberglied 1979), UV light in the bog will
be relatively greater than in other habitats where upper
vegetation absorbs some of the UV (Horn 1971). Vegetation
and soils in the bog selectively absorb or reflect UV, and
generally appear under spectrophotometry as a random mixture
of varying reflectance qualities.

The dominant ground cover is Sphagnum imbricatum; plants
are densely packed to form a relatively smooth mat which
appears gold, brown and orange in the visible spectrum. Other
Sphagnum species are locally common and may form loose colonies
with colors that include pale green, red and yellow. At
close range, with UV photography, Sphagnum appears minutely
variegated; UV-absorbing leaves are dominant, with highlights
of strong reflectance in new buds. Low-lying vegetation includes
withered Scirpus cespitosus (highly reflectant), living sedges
(mostly absorbant), mud and decaying Sphagnum (usually strongly
absorbant), lichens (Cladonia spp.)(highly reflectant) and
vegetative parts of bog plants (varying reflectances). At a

range of less than 2 m, slight differences in reflection were discernible, but as the distance increases between the photographer and the vegetation, these distinctions become less evident. Distant vegetation, including Sphagnum hummocks, bog plants, scattered lodgepole pine, pine forest and the horizon, appears as monotone blocks of low UV reflectance.

UV reflectance in the microhabitat

The types of vegetation and soils on the bog, and their UV reflectant qualities, were not uniform throughout the habitat, and thus the dominant backgrounds (at the same plane as the corolla) varied between species (Table 3). Those corollas that rested close to a Sphagnum substrate showed little difference in UV reflectance with their backgrounds. At close range (less than 1 m), UV-absorbing petals stood out only moderately as a monotone reflectance against a variegated background. At a greater distance, the outer border of the corollas of Gentiana douglasiana, Coptis trifolia and Trientalis europaea and the immediate backdrop of Sphagnum were difficult to distinguish. Andromeda polifolia and Vaccinium oxycoccus were only slightly conspicuous by comparative reflectance, as

the sepals and corolla-tips in the former and the anthers
in the latter are moderate UV reflectors. In Loiseleuria
procumbens, the mat of closely spaced leaves form a back-
ground similar in UV reflection to the corollas. The flower
clusters of Tofieldia glutinosa and Ledum palustre have
various backgrounds on the same plane as the corollas, including
Sphagnum and bog vegetation at various distances, and

the distant pine forest, all of which offer little contrast
with the corollas. Rubus chamaemorus is subtended by one
or two UV-reflecting leaves which form one-half of the back-
ground, the other half being Sphagnum imbricatum, creating
moderate contrast among the 3 monotone reflectances. The
corollas which reflect strongest in UV (Kalmia polifolia,
Anargidium boreale, Fauria crista-galli) have backgrounds
of blocks of primarily absorbing vegetation (distant forest)
which contrast with the corollas.

In visible light, most flower species and their backgrounds
are of contrasting hues at close range. A. boreale, K. polifolia,
L. palustre and F. crista-galli are visually conspicuous from
a distance of greater than 5 m, while the remaining cannot be
discerned until the observer is within about 2 m. C. trifolia
is difficult to distinguish from its background at close

range, expecially when S. cespitosus is common in the
microhabitat.

Discussion

Analysis of individual bog flowers showed that high
UV reflectance is not a dominant component of floral color-
ation. Rather, its expression is important as it accentuates
the reproductive parts of the flower. Contrasting UV reflectance
in pistils, stamens and nectaries, as well as concentric
bands of alternating reflectance, could function as effective
nectar guides to direct pollinators to food rewards (Knoll
1922, Manning 1956). Such "invisible" guides, in which
UV-absorbing details contrasted with predominantly UV-reflecting
corollas, have been recognized in numerous studies (Kugler
1943, Daumer 1958, Horovitz and Cohen 1972, Mulligan and
Kevan 1973, Thorpe et al. 1975). However, in the bog species
studied, the reverse pattern (reflecting guides against
absorbing corollas) was more common. Nectar guides are
effective from short distances from the flower or after
the insect has alighted (Knoll 1922, Manning 1956). Whether
reflectant UV guides are highly visible to pollinators over

range, especially when <u>S. cespitosus</u> is common in the microhabitat.

Discussion

long distances, due to the greater acuity of insect vision in this waveband, is unknown.

The most common flower colour on the bog was UV-absorbing white (5 species). In a study of high Arctic flowers, Kevan (1972) found a similar proportion (49%) of visibly panchromatic species. Since pollinator visits were low, he concluded that this coloration is "unattractive" to insects. On the bog, UV-absorbing white flowers were visited by numerous dipteran pollinators, although bumblebee visits were rarely observed. Although neither this study, nor Kevan's (1972) investigated nocturnal or crepuscular pollinators, it is probable that visibly white flowers are pollinated by moths. At low light levels (dusk, moonlight and dawn), these flowers are conspicuous against their backgrounds, at least to human visual perception, compared to violet/red or yellow species.

UV patterns within flowers were distinct, not by absolute surface area, but by contrast with adjacent or background reflections. In the micro-habitat in which a flower appears to a pollinator, one might expect similar contrasting UV patterns between flowers and backgrounds. Among the bog species that had UV-absorbing petals, there were no obvious

juxtapositions in the degree of UV reflection between inflorescences and their backgrounds. Even assuming disproportionate acuity in UV by insects, the symmetry of nectar guides in flowers that lay close to their substrate was similar to symmetry in background reflectances (most strongly expressed in Sphagnum buds and Empetrum nigrum). Among large, UV-reflectant species, there was moderate to high contrast with their backgrounds.

UV reflectance patterns in bog flowers function within corollas to advertise food rewards and direct pollinators over short distances. For long-range conspicuousness, there appeared to be graded degrees of visibility, ranging from large, highly reflectant targets to small, UV-absorbing white flowers.

Pollinators are not indiscriminate on the bog. Bombus workers and queens showed preferences for the large UV-reflecting flowers that contrasted with their backgrounds, while small dipterans (including syrphids) visited the less conspicuous inflorescences. (Table 4). The low density of the UV-reflecting flowers necessitates a pollinator, like Bombus, that is a strong flyer that will consistently carry pollen over long

distances to flowers of the same species. The UV responsive-
ness of bees and their flower fidelity has been well demon-
strated (Heinrich 1974).

Smaller flowers, which on the bog are pollinated by
dipterans, may be unsuited to Bombus visits; delicate
reproductive organs may be mutilated during foraging, and
minute food rewards be quickly depleted by the larger
pollinator. Long-range inconspicuousness, demonstrated by
UV-absorbing flowers against predominantly UV-absorbing back-
grounds, may have an advantage in excluding such undesirable
pollinators.

Dipterans are generally low in flower faithfulness and
because of their small size and weak flying ability cannot
transport great pollen loads over long distances (van der Pijl
and Faegri 1979). With such pollinators, clustering of plants
may be advantageous as movement from flower to flower is
easily accomplished, and nectar guides would be effective
from within the dense plant clusters. Dipterans are numerous
on the bog, and the likelihood of encounters with flower
groups is high, thus compensating for the lack of long-range

visual attraction.

Although other factors, such as odour, movement, and
specific visible colours, may contribute to the visibility
of bog flowers, graded degrees of UV conspicuousness may be
important in exploiting the pollen-carrying capabilities
of various pollinators.

	petal	stigma	style	ovary	nectary	filament	anther
Loiseleuria procumbens	0	5.0	-	-	-	0	0
Coptis trifolia	0	pistil 3.5			1.0	0	3.5
Andromeda polifolia	0	sepals & corolla tips 3.0				-	-
Rubus chamaemorus	2.0	-	-	-	-	0	4.0
Kalmia polifolia	2.0	3.5	0	2.0	4.0	0	0
Gentiana douglasiana	0	0	0	-	4.0	-	4.0
Fauria crista-galli	5/0	4.0	4.0	-	corolla tube 0		-
Trientalis europaea	0	3.5	3.5	3.5	4.0	3.5	3.5
Ledum palustre	0	0	0	0	3.5	3.5	3.5
Apargidium boreale	5/0	0	0	-	-	-	0
Vaccinium oxycoccus	0	0	0	sepals 5	-	-	3.5
Tofieldia glutinosa	0	1.0	1.0	-	3.5	0	3.5

** In the final draft, Table 1 and Plate 1 will be replaced by black and white plates showing UV reflectance in all 12 species.

Table 2. Growth habits. Mean measurements.

	height (cm)	corolla size (mm)	density (m^2)	corolla orientation
Loiseleuria procumbens	10	5	25	horizontal
Coptis trifolia	4	15	15	horizontal
Andromeda polifolia	10	10	25	
Rubus chamaemorus	10	20	10	horizontal
Kalmia polifolia	30	20	8	vertical
Gentiana douglasiana	10	15	31	horizontal
Fauria crista-galli	18	20	3	vertical
Trientalis europaea	5	15	21	horizontal
Ledum palustre	50	10	28	various
Apargidium boreale	18	40	2	vertical
Vaccinium oxycoccus	2	10	27	
Tofieldia glutinosa	25	8	13	various

Table 3. UV reflectance of dominant backgrounds of bog flowers at the same
plane as corolla. Reflectance values as in Table 1.

	Sphagnum 0/5	lichens 5	dead grass 5	living sedges 0	species leaves 0-5	other leaves 0-5	distant vegetation 0-3	mud/earth 0
L. procumbens					X			
C. trifolia	X	X	X					X
A. polifolia	X				X			
R. chamaemorus	X				X			
K. polifolia							X	
G. douglasiana	X		X	X				
P. crista-galli							X	
T. europaea	X			X	X			
L. palustre	X		X	X	X		X	
A. boreale							X	
V. oxycoccus	X					X		
T. glutinosa	X						X	

Table 4. Principle pollinators of bog flowers.

Bombus ssp.	Syrphidae	small dipterans
Aparzidium boreale	Loiseleuria procumbens	Tofieldia glutinosa
Kalmia polifolia	Gentiana douglasiana	Coptis trifolia
	Andromeda polifolia	Trientalis europaea
	Vaccinium oxycoccus	Rubus chamaemorus
		Ledum palustre
		Loiseleuria procumbens
		Gentiana douglasiana

Caption to Figure 1

Ultraviolet pattern in bog flowers. a,b - Coptis trifolia
(×2); c,d - Aparsidium boreale (×2); e,f - Gentiana
douglasiana (×⅓) in habitat. a,c & e show reflection of
visible light; b,d & f show UV reflection. Position of
flowers in f are indicated by arrows.

Acknowledgements

E   **VISIBLE**   F   **UV**