Drizzle Lake

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ULTRAVIOLET COMPONENTS OF FLOWER COLOR IN A BOG HABITAT

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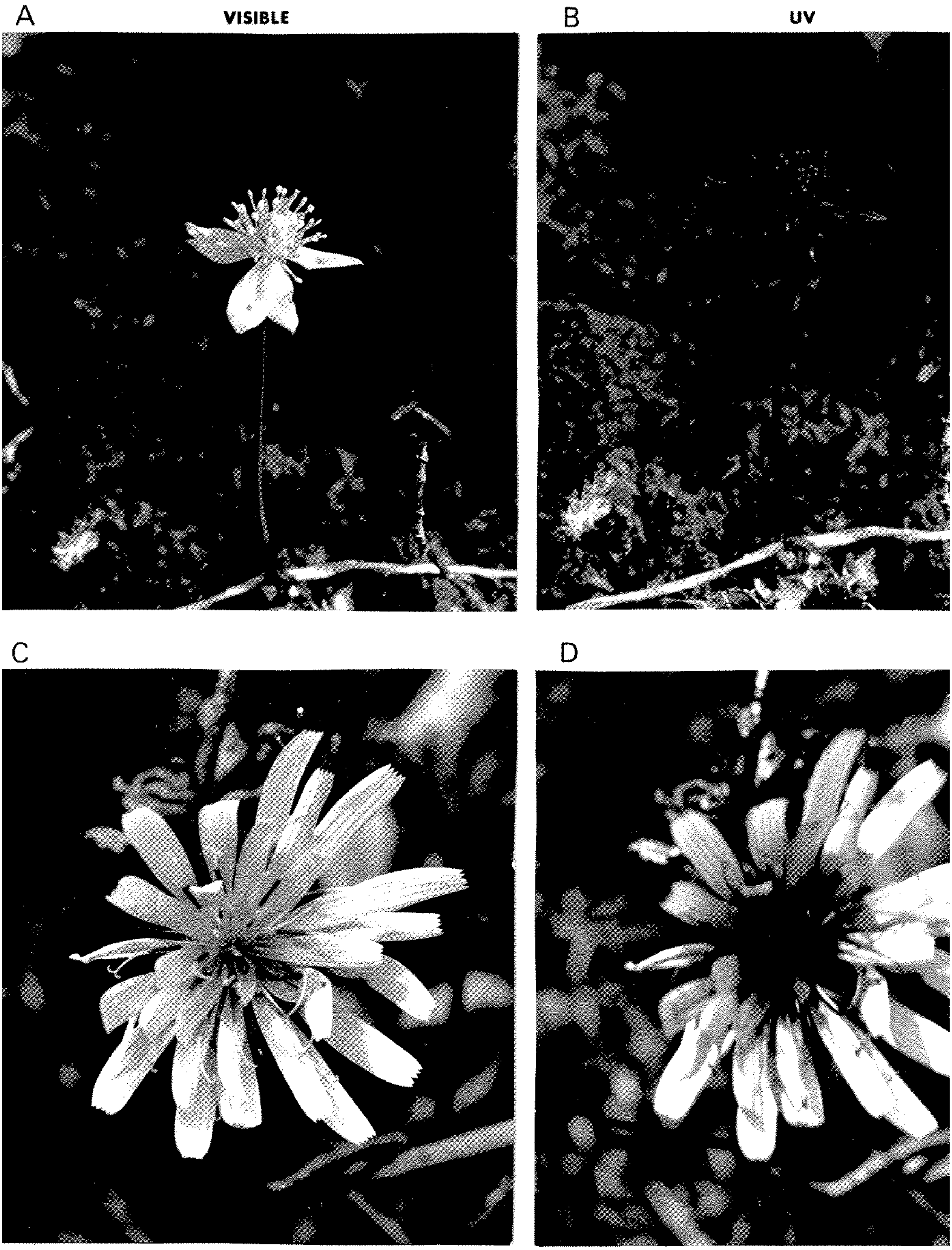
A
VISIBLE
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UV
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Introduction

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 $m\mu$, coloration of flowers and backgrounds in the visible spectrum is referred to as well.

Methods

Floral reflectance in longwave ultraviolet (350-400 $m\mu$) 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 $m\mu$) 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 heighth, 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. Anecdotal 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 bog flowers (Table 2) 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/m^2), while those with larger corollas (>20 mm) were solitary or partially clustered (<4/m^2). 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 background 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 background, the other half being Sphagnum imbricatum, creating moderate contrast among the 3 monotone reflectances. The corollas which reflect strongest in UV (Kalmia polifolia, Apargidium 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 coloration. 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 S. cespitosus 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 responsiveness of bees and their flower fidelity has been well demonstrated (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 backgrounds, 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.

**Table 1. UV reflectance within flowers, graded on a scale of 0-5, with 0 indicating complete UV absorbance and 5, high reflectance. Species are listed in order of flowering phenology. – : parts not revealed.

	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				
F. crista-galli							X	
T. europaea	X				X			
L. palustre	X		X	X	X		X	
A. boreale							X	
V. oxycoccus	X							
T. glutinosa	X					X	X	

Table 4. Principle pollinators of bog flowers.

Bombus ssp.	Syrphidae	small dipterans
Apargidium 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 ($\times 2$); c,d - Apargidium boreale ($\times 2$); e,f - Gentiana douglasiana ($\times \frac{1}{3}$) 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.

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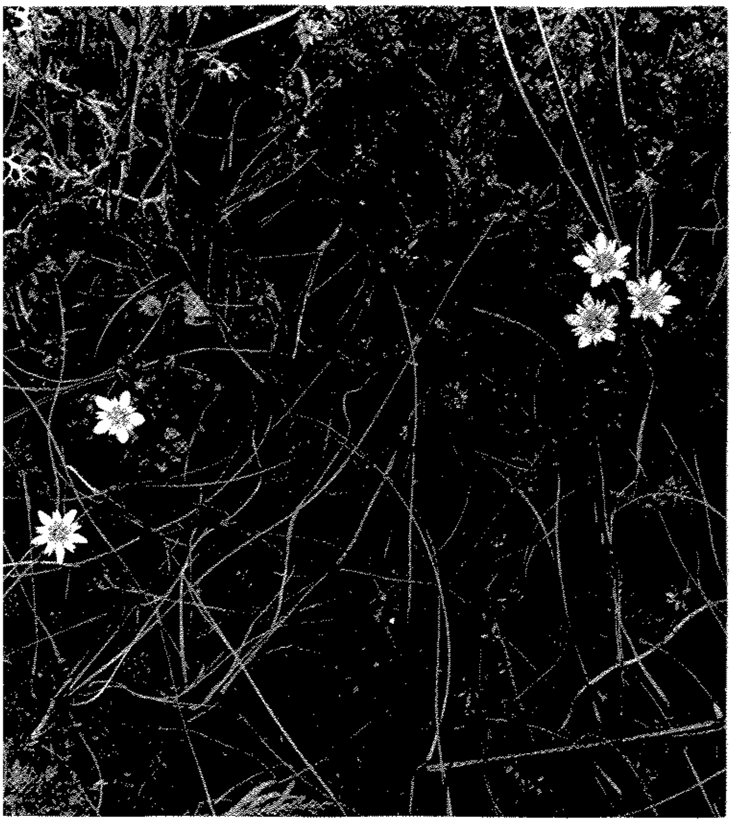
E **VISIBLE**



F **UV**