ULTRAVIOLET REFLECTANCE AND ABSORPTION PATTERNS IN FLOWERS OF NYMPHAEA ALBA L., NYMPHAEA CANDIDA PRESL AND NUPHAR LUTEA (L.) Sm. (NYMPHAEACEAE)*

Th.G. GIESEN and G. VAN DER VELDE

Laboratory of Aquatic Ecology, Catholic University, Toernooiveld, 6525 ED, Nijmegen (The Netherlands)

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ABSTRACT

Giesen, Th.G. and Van der Velde, G., 1983. Ultraviolet reflectance and absorption patterns in flowers of Nymphaea alba L., Nymphaea candida Presi and Nuphar lutea (L.) Sm. (Nymphaeaccac). Aquat. Bot., 16: 369-376.

Ultraviolet (u.v.) patterns of flowers of Nymphaeaceae as an important colour component for flower-visiting insects have been totally neglected in studies of their floral biology. The three day-flowering species studied show distinct u.v. patterns. Both Nymphaea species show high absorption in the centre of the flowers and u.v.-reflective thecae. In Nymphaea alba L. a radial u.v. stripe reflection pattern is visible on the stigmatic disc in u.v. photographs, which is weakly developed in Nymphaea candida Presl flowers. The flowers of Nuphar show the most distinct u.v. reflection pattern in the form of a circle formed by the u.v.-reflective tips and filaments of the stamens, in contrast to the shiny petals and u.v.-absorptive stigmatic disc, thecae and sepals.

INTRODUCTION

Ultraviolet reflection and absorption are important components of flower colour, as most flower-visiting insects such as bees and flies are highly sensitive to ultraviolet (u.v.) light (Mazokhin-Porsnyakow, 1959).

The insect eyes show a high peak of response to u.v. light and a lesser one in the green to yellow part of the spectrum (Kevan, 1978). These and other colour patterns, together with the shape of the flower, attract the insects from a distance and aid them to quickly recognize flowers of the same species. Ultraviolet patterns also have a taxonomic value (Kevan, 1978).

In studies on the floral biology of Nymphaeaceae the u.v. patterns of the flowers have been completely neglected, even in recent studies of the day-flowering species such as Prance and Anderson (1976), Schneider and Moore (1977), Meeuse and Schneider (1979/80), Schneider and Buchanan (1980), Schneider and Chaney (1981), Schneider and Jeter (1982) and

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Schneider (1979, 1982a,b). It is known that bees and flies are important flower visitors.

Ultraviolet photographs of flowers of three species: Nymphaea alba L., Nymphaea candida Presl and Nuphar lutea (L.) Sm., all collected in The Netherlands, are presented here to fill this gap in our knowledge of the floral biology of Nymphaeaceae.

METHODS

Ultraviolet photographs (black and white film Agfapan 100 ASA, Schott-Filter U.G. 1, penetration between 300-400 nm and 680-1000 nm) have been made of flowers of Nymphaeaceae in sunlight from 12.00 to 14.00 h. The exposure time and diaphragm diameters were determined with the aid of an exposure meter, with U.G. 1 filter. To obtain a higher contrast the film has been developed 20% longer than normal.

RESULTS

From the u.v. photographs presented in Figs. 1—4, it is obvious that the flowers of the three species of Nymphaeaceae studied, differ not only in shape and in the case of Nymphaea and Nuphar visible colours, but also with respect to their u.v. pattern.

Nymphaea

Nymphaea candida and Nymphaea alba are both white-flowering species, with yellow thecae and stigmatic disc. The shapes of the flowers differ, as those of N. candida are apparently not as widely opened as those of N. alba.

On the u.v. photographs of flowers of both species the petals and sepals are reflective. In the case of N. candida there are heavy shadow patterns caused by the more upright position of petals and sepals. Because of this, the tips of the petals and sepals show much more reflection as compared to those of N. alba. Richtmeyer (1923) stated that reflection in white flowers can exist only by shining. According to Kugler (1963) shining occurs at the outerside of the epidermis cells, while diffuse reflection originates from layers of membranes and intercellular air deeper in the tissue.

The yellow thecae of both species, however, reflect u.v. light in the same amount and the position of the anthers is very important with respect to this. The anthers bend over the stigmatic disc when they are ripening during successive flowering stages (Figs. 1 and 2). The thecae of the inner rows of the stamens do not become more visible in N. alba.

In contrast to the filaments of Nuphar lutea flowers, the filaments of the stamens of both Nymphaea species show a heavy absorption of u.v. light, as the central part of the flower appears dark in the u.v. photographs. This central part functions clearly as a guidance system for insects, leading them

to the central part of the flower. This central u.v. absorption area is most obvious in flowers of N. alba (Fig. 1). In these flowers shadow patterns are not as heavy as in those of N. candida.

First-day flowers of Nymphaea show more contrast in their u.v. pattern, and are more conspicuous for flower-visiting insects (Kugler, 1938) than older flowers (Figs. 1 and 2).

The stigmatic disc of first-day flowers of N. alba shows a typical radial u.v. reflection pattern, consisting of alternating long and short stripes visible between and on the stigmatic rays. In N. candida flowers this pattern of stripes is weakly developed. There is in this species a u.v. absorption pattern visible in the centre of the stigmatic disc.

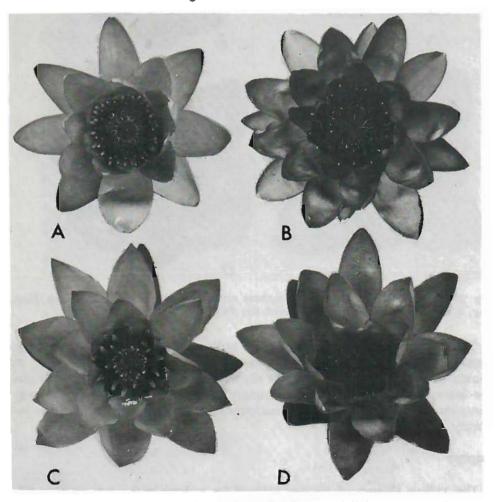


Fig. 1. Ultraviolet photographs of Nymphaea alba flowers of different age. A. First-day; B. second-day; C. third-day (with very obvious eggs of the fly Notiphila brunnipes R.-D.); D. fourth- or fifth-day flower.

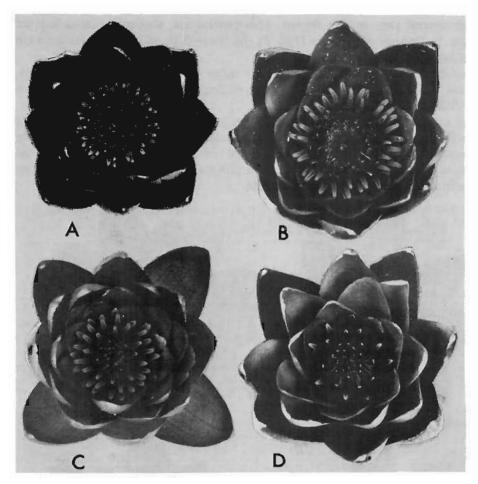


Fig. 2. Ultraviolet photographs of Nymphaea candida flowers of different age. A. Firstday; B. second-day; C. third-day; D. fourth-day flower.

The contrast between the flowers of both species and their surroundings (water surface and floating and/or aerial leaves) is also very obvious, as shown in Fig. 3. The water surface shows a moderate u.v. reflection, while the leaves reflect u.v. light very strongly. Thus, the flowers must be very conspicuous within their direct surroundings as spots with a low u.v. intensity.

Nuphar

The yellow flowers of Nuphar lutea show a shape and a u.v. pattern different from those of Nymphaea species (Fig. 4).

The tips of the anthers are very strongly u.v. reflective, in contrast to the other flower parts, showing only shining (petals) and absorption (sepals, stigmatic disc).



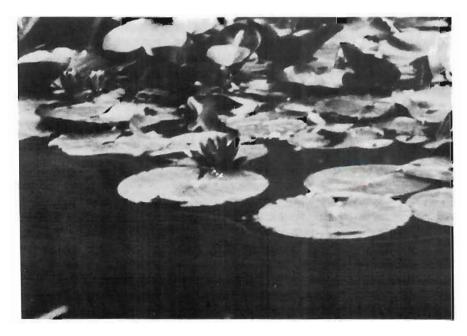


Fig. 3. Ultraviolet photographs of Nymphaea alba flowers and surroundings.

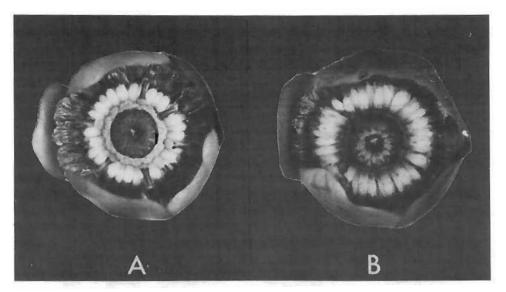


Fig. 4. Ultraviolet photographs of two stages of a Nuphar lutea flower. A. Third-day; B. fifth-day flower.

First-day flowers, however, are still nearly closed with only a triangular opening above the stigmatic disc (Schneider and Moore, 1977). Thus, the u.v. pattern is not visible in that stage. However, a flower on the second day of flowering must be very conspicuous for a u.v. sensitive insect.

The u.v. reflective circle around the stigmatic disc, formed by the u.v. reflective tips of the anthers, remains during the recurving of the anthers in later stages. The filaments of the anthers, in contrast to their thecae, are also very u.v. reflective (Fig. 4b). Because of this, insect visits must be frequent in later stages of flowering when large amounts of pollen are available even though the stigmatic disc is no longer receptive and nectar production is reduced.

DISCUSSION

Ultraviolet patterns of the flowers of the Nymphaeaceae species studied certainly play an important role in the attraction of flower-visiting insects, especially bees, syrphids and ephydrid flies such as *Notiphila brunnipes* R.-D. (Van der Velde and Brock, 1980).

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The u.v. absorbing flowers of the Nymphaeaceae in contrast to the high u.v. reflection of their floating leaves must be very attractive to insects, as they are attracted by spots with a high absorption of u.v. light (Daumer, 1958).

Nuphar flowers are visited by many more insect species (44) than Nymphaea flowers (24) (Van der Velde et al., 1978). (Nymphaea candida was only studied at a very exposed locality, resulting in only 14 species of

flower visiting insects.) It can, however, be expected that the Nymphaea candida flowers are less attractive for insects as they are not so colourful as the Nymphaea alba flowers by the shadow patterns as mentioned before.

The differences in the numbers of flower-visitors can, only partly be ascribed to differences in u.v. patterns of the flowers which attract distant insects. The combination of yellow and yellow-ultraviolet (bee-purple) as in *Nuphar* flowers must also be very attractive, as the insect eyes are highly sensitive for both (Kevan, 1978; Brantjes, 1979).

There are, however, more attractive features of the flower than colour alone, such as the shape of the flower, odour (only in the case of *Nuphar*), the presence of nectar (*Nuphar*) or stigmatic exudate (*Nymphaea*), pollen and higher temperatures (Van der Velde and Brock, 1980).

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REFERENCES

Brantjes, N.B.M., 1979. Bloemenkleur bij zonneschijn. Vakbl. Biol., 59: 396-403. Daumer, K., 1958. Blumenfarben wie die Bienen sie sehen. Z. Vgl. Physiol., 41: 49-110.

Kevan, P.G., 1978. Floral coloration, its colorimetric analysis and significance in anthecology. In: A.J. Richards (Editor), The Pollination of Flowers by Insects. Linnean Society Symposium Series, No. 6, Linnean Society of London, Academic Press, London, pp. 51-78.

Kugler, H., 1988. Blütenökologische Untersuchungen mit Hummeln IX. Die optische Nahwirkung von natürlichen Blüten und Blütenstanden. Planta, 29: 47-66.

Kugler, H., 1968. U.V. — Musterung auf Blüten und ihr Zustandekommen. Planta, 59: 296-329.

Mazokhin-Porsnyakow, G.A., 1959. Reflection of ultraviolet rays by flowers and insect vision. Entomol. Rev., 38: 285-296.

Meeuse, B.J.D. and Schneider, E.L., 1979/80. Nymphaea revisited: a preliminary communication. Isr. J. Bot., 28: 65-79.

Prance, G.T. and Anderson, A.B., 1976. Studies on the floral biology of neotropical Nymphaeaceae. 3. Acta Amazonica, 6: 163-170.

Richtmeyer, F.K., 1923. The reflection of ultraviolet by flowers. J. Optical Soc. Am. et Rev. Scient. Instruments, 7: 151-168.

Schneider, E.L., 1979. Pollination biology of the Nymphaeaceae. Proc. IVth Int. Symp. on Pollination, Md. Agric. Exp. Stn. Spec. Misc. Publ., 1: 419-429.

Schneider, E.L., 1982a. Notes on the floral biology of Nymphaea elegans (Nymphaeaceae) in Texas. Aquat. Bot., 12: 197-200.

Schneider, E.L., 1982b. Observations on the pollination biology of Nymphaea gigantea W.J. Hooker (Nymphaeaceae). West. Aust. Nat., 15: 71-72.

Schneider, E.L., and Buchanan, J.D., 1980. Morphological studies of the Nymphaeaceae, XI. The floral biology of *Nelumbo pentapetala*. Am. J. Bot., 67: 182-193.

Schneider, E.L. and Chaney, T., 1981. The floral biology of Nymphaea odorata (Nymphaeaceae). Southwest. Nat., 26: 159-165.

- Schneider, E.L. and Jeter, J.M., 1982. Morphological studies of the Nymphaeaceae. XII. The floral biology of Cabomba caroliniana. Am. J. Bot., 69: 1410-1419.
- Schneider, E.L. and Moore, L.A., 1977. Morphological studies of the Nymphaeaceae VII. The floral biology of *Nuphar lutea* subsp. macrophylla. Brittonia, 29: 88-99.
- Van der Velde, G., Brock, Th.C.M., Heine, M. and Peeters, P.M.P.M., 1978. Flowers of Dutch Nymphaeaceae as a habitat for insects. Acta Bot. Neerl., 27: 429-430.
- Van der Velde, G. and Brock, Th.C.M., 1980. The life history and habits of *Notiphila brunnipes* Robineau-Desvoidy (Diptera, Ephydridae), an autecological study on a fly associated with nymphaeid vegetations. Tijdschr. Entomol., 123: 105—127.