so deep that winnowing or erosion has left large gaps in the sedimentary record.

It is clear that the silt mean in cores 74 and 251 during the last ice age was coarser than at present (Fig. 2), an indication of a higher current velocity 18,000 years B.P. It is not possible to interpret the silt mean as a simple function of bottom current velocity; however, the relative increase in particle size in both cores may be used to infer a relative increase in velocity. In core 74 the silt mean 18,000 years B.P. is 5.3 ϕ compared to the present silt mean of 5.5 ϕ. The silt mean coarsened from 5.9 ϕ to 5.65 ϕ in core 251 during the last ice age. The magnitude of the change in the silt mean is nearly the same in both cores; this finding suggests a similar relative increase in bottom current velocity on both sides of the channel. Therefore, the particle size data suggest an increase in AABW velocity during the last ice age, although we cannot estimate the magnitude of the change.

Particle size analysis of sediment from 18,000 years B.P. indicates that the combined effects of a shallower LNM and possibly increased velocity of bottom water resulted in an increase in AABW transport through the Vema Channel during the last glacial maximum. Our approach has provided a semiquantitative method by which to interpret changes in bottom water production during the past. If demonstrated to be worldwide in extent, this increased transport conceivably could be the cause of widespread erosional disconformities which have been suspected to be associated with Neogene glaciations (*16*).

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Appearance of Vegetation in Ultraviolet Light: Absorbing Flowers, Reflecting Backgrounds

Abstract. *Flowers that uniformly absorb ultraviolet light may contrast strikingly with a bright ultraviolet-reflecting background, such as densely hairy or glaucous foliage, white soils, or the sky. Shadows will not resemble these flowers if the appearance of each in visible light is also considered. Examples are shown from Mexican heliotropiums and Michigan dune plants.*

Since the realization that insects use ultraviolet (UV) reflectance patterns in searching for flowers, such patterns have been extensively studied (*1*). However, little note has been taken of the background against which the flowers are normally viewed. Usually the background is tacitly assumed to absorb UV light, and published photographs generally have dark gray or black backgrounds. Thus, flowers that do not reflect UV seem uninteresting. In fact, some natural backgrounds are highly reflectant of UV, and flowers that absorb UV contrast strikingly with them.

To facilitate interpretation of photographs taken with visible (to the human eye) and UV light, I equalized the contrast and standardized the exposures, so that equal percentages of reflectances result in approximately equally bright images (*2*). In the pictures taken with ringflash illumination (*3*) the distant background appears to be black as a result of the rapid decrease of light intensity with increasing distance from the flash; however, the brightness of objects near the focal plane can be compared. The pictures taken with daylight illumination show much more realistic appearances.

I first encountered the pattern of a dark flower against a bright background in Mexico during a study of *Heliotropium* section *Orthostachys* and sect. *Halmyrophila*. The small flowers of these plants are positioned close to the leaves so that a plant's foliage constitutes much of its flower's background. In visible light these flowers are white with a yellow or yellow-green center. The densely hairy or glaucous leaves, stems, sepals, and bracts are whitish-green or green. Most of these species have UV images showing dark flowers and bright foliage. An animal whose color vision includes UV will see the flower as a brightly colored spot rich in visible light and poor in UV. The foliage will appear white or pastel owing to its high reflectance at all wavelengths (Figs. 1 and 2).

Some plants that expose part of the back of the corolla in bud have a UV pattern that looks like sepals on the early exposed corolla parts and one that looks like a flower on the parts exposed at opening. In other examples (*4*) the sepals were UV-absorbing and the flower was mostly reflecting. Some species of *Heliotropium* show the same phenomenon but with the colors reversed. Here a row of hairs makes the early exposed rear portions of the corolla highly reflectant in the UV, while the hairless remainder is dark (Figs. 3 and 4). On the foliage as well, the hairs (or glaucous covering) are responsible for the bright UV reflection. The actual leaf surface reflects little UV.

Since sand provides a UV-reflecting background, I took photographs of sand dune vegetation near Lake Michigan in the hope of finding more plants with the dark-flower UV pattern. A number of additional examples were found and three are shown (Figs. 5–7). The dune pictures were taken with daylight illumination on sunny days and so include shadows. The shadows are less depleted of UV light than of visible light, since the very bright UV from the "blue" sky partly fills in the sunlight shadows. Therefore, the shadows do not resemble UV-absorbing flowers; the shadow illumination is more or less complementary in hue to flowers that reflect visible but not UV light. This effect is most striking when the sun is low in the horizon, but it vanishes in cloudy weather, when shadows are equally depleted of visible and UV light.

The UV appearance of some flowers as seen in daylight can be misinterpreted in ringflash photographs. Some flowers reflect UV only by shininess, even though they reflect visible light diffusely. In daylight, such flowers generally appear UV-absorbing with a few brightly reflecting highlights. However, in some orientations, the flowers may appear to be very brightly reflecting under the symmetry of ringflash illumination. The close-up photographs of *Gypsophila paniculata* show this phenomenon (Figs. 10 and 11).

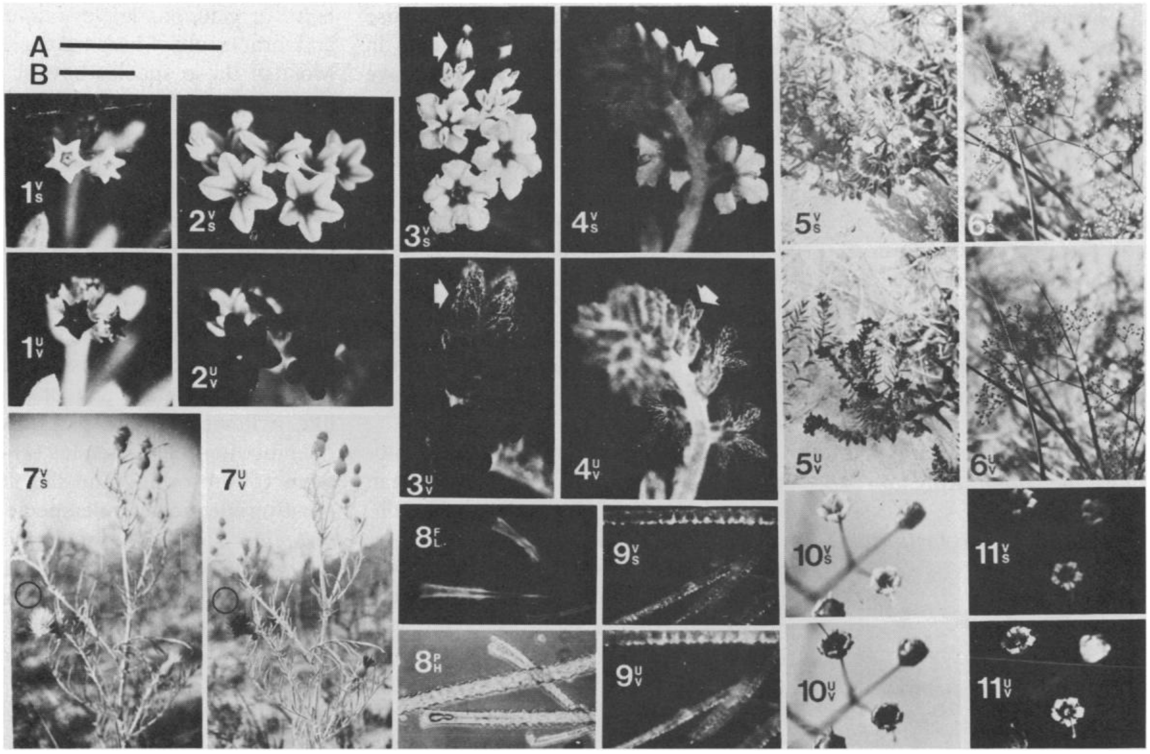
The difficulty of taking UV pictures would make an easier method of detecting UV reflectance welcome. An indirect method in which fluorescence is used has been suggested. The UV-reflectance pattern of a flower is often replicated by the visible fluorescent pattern produced by dried herbarium specimens illuminated by UV (*5*).

In *Heliotropium curassavicum* the glaucous foliage does not fluoresce at all, but in the other species of *Heliotropium* studied here the hairs fluoresce brilliantly, while the corollas fluoresce weakly if at all. Thus, for these species (but not for *H. curassavicum*) the fluorescent and UV-reflectance patterns are similar.

The simple structure of the hair provides an opportunity to determine whether the UV reflection is related to the UV-excited fluorescence. The hairs are unicellular with thick silicified secondary walls and numerous large blunt conical papillae on the outer surface. The bright fluorescence is confined to the inner wall layers near the base of the hair, but the UV reflectance is caused by reflection and refraction at all the surfaces of the hair, like the visible light reflectance. The high index of refraction of the hairs (≈ 1.54) enhances the efficiency of reflection. Thus, the UV reflectance is not related to the fluorescence. Their association in this case may be a coincidence (Figs. 8 and 9).

These UV-reflecting hairs should not be confused with the ridged, more or less hair-shaped, UV-absorbing cells in the floral epidermises of a number of plants (*6*). The corolla surface in *Heliotropium* is covered with similar ridged cells, which are sometimes elongated into hairs and which (at least in *H. procumbens*) appear to have flavonoids concentrated in their tips (*7*). Unlike the UV-reflecting hairs, the ridged cells in *Heliotropium* have thin unsilicified primary cell walls; they are also much smaller than the UV-reflecting hairs.

The striking appearance of all these



Figs. 1–11. Photographs of plants in the visible spectrum (VS) and in ultraviolet light (UV). Ringflash illumination for Figs. 1–4 and 11; daylight illumination for Figs. 5–7 and 10. Scale: *A* represents 1 cm for Figs. 1–4, 10, and 11; *B* represents 100 μm for Figs. 8 and 9. Fig. 1. *Heliotropium calcicola*, an extremely hairy plant. Fig. 2. *Heliotropium curassavicum*, a glaucous plant. Fig. 3. *Heliotropium ternatum*, hairs on the folded tips of the corollas reflect UV (arrow); expanded corollas absorb UV. Fig. 4. Back of the inflorescence shown in Fig. 3. A row of hairs on each corolla lobe reflects UV. The hairless parts of the corolla absorb UV. On the half-open flower (arrow) only the UV-reflecting portions are exposed. Fig. 5. *Lithospermum carolinense*: shadows in the UV picture are much fainter than those in the VS picture since these pictures were taken just before sunset. The intensity of UV divided by that of visible light is 30 percent greater in the shadow than the sunlight areas. (Ratios of reflected light intensity: flower/sunlit sand background: VS 1, UV 0.08; flower/sand background in shadow: VS 2.7, UV 0.17; flower/foliage: VS 2.4, UV 0.5. The flowers appear yellow to human viewers.) Fig. 6. *Gypsophila paniculata*: an introduced species forming a large population on the Michigan sand dune. The flowers appear white to human viewers. Fig. 7. *Circium pitcheri*: to human viewers the flowers appear cream-colored and vegetative parts of the plant appear greenish white. The species is endemic to the sandy shores of the Great Lakes. Note the extremely bright appearance of the sky in UV. (Ratios of reflected light intensity: flower/circled background: VS 2, UV 0.3; flower/sky: VS 0.7, UV 0.01.) Fig. 8. Hairs of *Heliotropium fallax* var. *hintonii* viewed with phase contrast (PH) and with UV-excited fluorescence (FL). Parts of some hairs fluoresce. Fig. 9. Dry hairs from the same plant as in Fig. 8 viewed in reflected light. The distribution of reflected light is the same in visible as in UV light, which indicates that the UV light is reflected in the same way as the visible light. Fig. 10. *Gypsophila paniculata*: daylight illumination. Fig. 11. The same flowers as in Fig. 10 photographed with ringflash illumination.

various UV-absorbing flowers as viewed against their UV-reflecting backgrounds shows that the appearance of the habitat cannot be ignored in studying the UV-reflectance patterns of flowers. Shadows resulting from direct illumination by sunlight add additional complexity that may be important. The best way to observe the patterns is to photograph the plants in the field with natural daylight illumination. The use of more convenient methods such as flash photography or the fluorescence of dried material can lead to misinterpretation. The pattern of UV-absorbing flowers with UV-reflecting backgrounds can be expected in places with UV-reflecting soils or places with many hairy or glaucous plants.

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8. I thank R. C. Rollins for help and encouragement at all stages of this project, R. Silberglied for valuable discussions, R. Silberglied, E. S. Barghoorn, and J. E. Dowling for the use of equipment, R. E. Umber and T. Swain for help with phytochemistry, L. E. Morse for editorial assistance, N. G. Miller for his comments on the manuscript, and B. Hallberg for assistance in Mexico. Supported in part by NSF grant number GB 27911, R. C. Rollins, Principal Investigator, Harvard University.

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Submergent Macrophytes: Growth Under Winter Ice Cover

Abstract. *Densities of 26 submergent macrophyte species were determined in situ regularly for 3 years by individuals using self-contained underwater breathing apparatus (scuba). Although most of these species grew only during the summer, ten maintained high population densities and productivity throughout the winter. Maximum winter photosynthetic activity was 10 to 20 percent of summer rates. Extensive productivity of submergent aquatic plants under winter ice cover has not been well documented.*

The adaptation of self-contained underwater breathing apparatus (scuba) for scientific investigations has provided opportunities for in situ study of poorly accessible habitats such as the freshwater lake during winter ice cover. Most lakes and ponds in temperate climates above 35°N latitude are covered with several centimeters of ice during the winter months. The effect of low light intensity, coupled with low water temperature, on the photosynthetic activity of rooted submergent plants is not well understood. Little is known about the physiological activity and abundance of aquatic plants that may overwinter in the vegetative state (*1*).

Changes in population densities of 26 species of rooted submergent macrophytes occurring in Lake George, New York, were observed from 1973 to 1976. Most showed seasonal density profiles, with growth beginning in the early summer and dieback occurring in the autumn. However, ten species did not die in the autumn but continued to be metabolically active under winter ice in 2°C water. Measurements were made in Smith Bay, which encompasses approximately a lake surface area of 6 ha. The littoral zone gradually slopes to a depth of 9 m, where rooted aquatic plants could still be found. A transect from a midpoint on shore was traversed from 1- to 12-m depth by the diver (R.B.S.). Routinely a bottom surface area of 1 ha was observed, with determinations of community species composition and relative species abundance made underwater at depth increments of 1 m (*2*).

The mean population densities for four species are presented in Fig. 1. Each point ranged within one order of magnitude. Densities are shown for the depth of greatest abundance for each species. Two species, *Najas flexilis* and *Vallisneria americana*, showed pronounced seasonal changes in density patterns. *Najas flexilis* germinated from seeds in early June and reached maximum population densities averaging ten plants per square meter at a depth of 3 m by mid-July. By mid-August the plants had produced seeds and had begun to die back. In mid-June *V. americana* sprouted from rhizomes. Densities averaging 100 plants per square meter were attained at a depth of 3 m by late August. By October

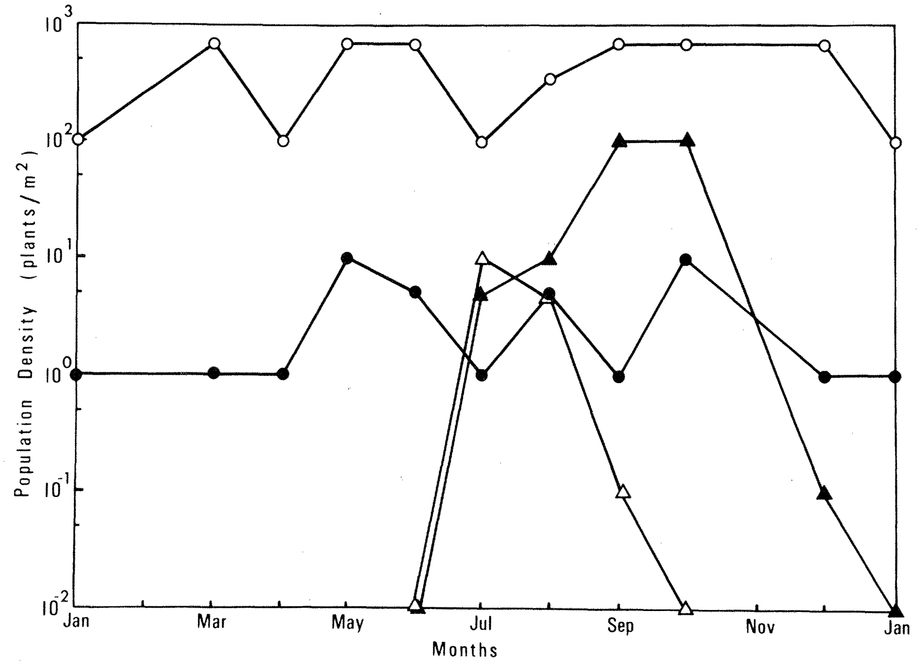

Fig. 1. Mean population densities of macrophyte species growing at depths of maximum abundance in Smith Bay, Lake George. ○, *Potamogeton robbinsii*, 5 m; ●, *Potamogeton amplifolius*, 3 m; △, *Najas flexilis*, 3 m; and ▲, *Vallisneria americana*, 3 m.