

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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References and Notes

1. To the bee, the appearance of the background is gray or dull gray [P. G. Kevan, *Can. J. Bot.* **50**, 2289 (1972)]. Foliage reflects little UV [G. A. Mazokhin-Porshnyakova, *Entomol. Rev. (USSR)* **38**, 285 (1959)]. See also, K. Daumer, *Z. Vgl. Physiol.* **41**, 49 (1958); H. Kugler, *Planta* **59**, 296 (1963); *Ber. Dtsch. Bot. Ges.* **79**, 57 (1966); T. Eisner, R. E. Silberglied, D. Aneshansley, J. E. Carrel, H. C. Howland, *Science* **166**, 1172 (1969); R. Ornduff and T. Mosquin, *Can. J. Bot.* **48**, 603 (1970); A. Horowitz and Y. Cohen, *Am. J. Bot.* **59**, 706 (1972); L. D. Guldberg and P. R. Atsatt, *Am. Midl. Nat.* **93**, 35 (1975). For information regarding techniques see R. E. Silberglied, *Funct. Photogr.* **11** (No. 2), 20 (1976); *ibid.* **11** (No. 3), 30 (1976).
2. All of these pictures were taken with a Kodak Wratten 18A filter and a glass lens (Nikkor 55-mm, *f*/3.5). In order to obtain approximately equal contrast, corresponding visible light and UV photographs were taken on the same roll of Tri-X film and printed with the same exposure and development on the same contrast grade paper. The slight difference in contrast due to the inherent difference in film response to visible and UV light (polycontrast effect) was ignored in making prints but was taken into account for quantitative calculations. Standard exposures were determined with the aid of reflectance standards and a densitometer (Macbeth TD 500). This standardization need be done only once for flash photography, but the variation in the amount of UV in daylight necessitates independent standardization for each daylight photographing session.
3. A ringlight is a circular xenon flashtube typically placed around the front of the camera lens and used primarily for closeup photography. It provides uniform, shadowless illumination.
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7. Flavonoids appear to be present in the petal parenchyma as well as in the tips of the ridged cells. The distribution of presumed flavonoids is based on fluorescence in dried sectioned corollas, which is enhanced by NH_3 and removed by extraction with methanol. Apigenin and luteolin glycosides have been identified by R. E. Umber in methanol extracts of corollas of this plant.
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 approxi-

mately 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

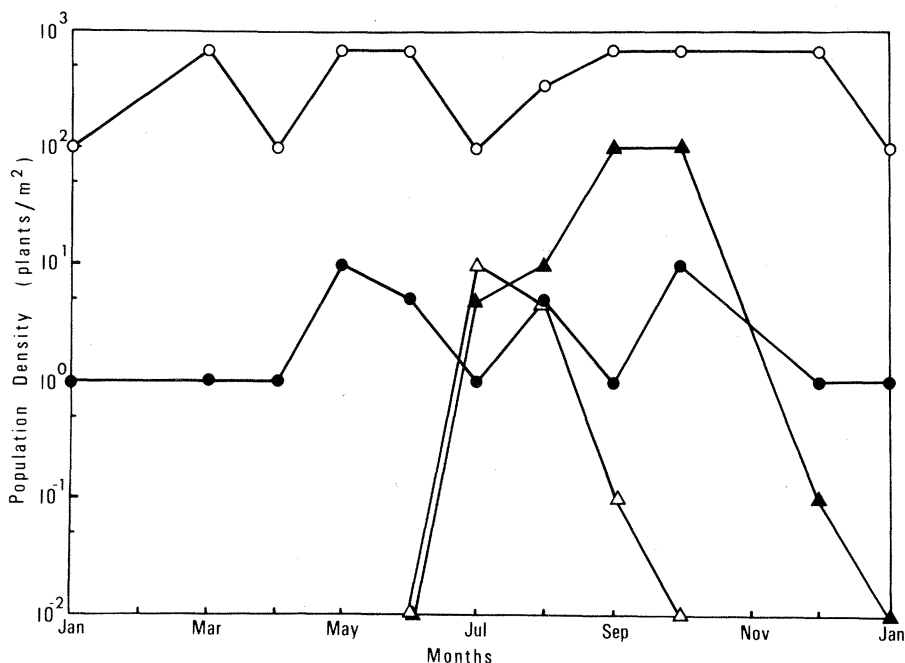


Fig. 1. Mean population densities of macrophyte species growing at depths of maximum abundance in Smith Bay, Lake George. ○, *Potamogeton robbinsii*, 5 m; ●, *Potamogeton amplifolius*, 3 m; △, *Najas flexilis*, 3 m; and ▲, *Vallisneria americana*, 3 m.

Table 1. Photosynthetic rates [milligrams of carbon per gram (dry weight) per hour] of submergent aquatic macrophytes that overwinter in a physiologically active vegetative state.

Organism	Photosynthetic rate			
	Midwinter		Midsummer	
	2°C	23°C	2°C	23°C
<i>Bidens beckii</i>	0.194 ± 0.076	1.02 ± 0.12	0.145 ± 0.037	1.22 ± 0.10
<i>Elodea canadensis</i>	0.368 ± 0.024	1.79 ± 0.13	0.192 ± 0.052	1.82 ± 0.17
<i>Isoetes echinospora</i>	0.166 ± 0.028		0.169 ± 0.011	0.920 ± 0.057
<i>Isoetes macrospora</i>	0.145 ± 0.021		0.088 ± 0.011	0.690 ± 0.035
<i>Myriophyllum alterniflorum</i>	0.323 ± 0.021	1.52 ± 0.10	0.145 ± 0.001	1.63 ± 0.18
<i>Myriophyllum tenellum</i>	0.042 ± 0.004	0.353 ± 0.208	0.070 ± 0.004	0.312 ± 0.045
<i>Potamogeton amplifolius</i>	0.210 ± 0.099	1.03 ± 0.212	0.153 ± 0.008	1.54 ± 0.20
<i>Potamogeton praelongus</i>	0.250 ± 0.071	1.48 ± 0.18	0.175 ± 0.035	1.50 ± 0.14
<i>Potamogeton robbinsii</i>	0.118 ± 0.055	0.433 ± 0.011	0.121 ± 0.016	0.805 ± 0.064
<i>Sagittaria graminea</i>	0.140 ± 0.028			0.820 ± 0.099

*Data are expressed as mean values ± the standard deviation.

new rhizomes were formed, and the vegetative plants began to die. Population densities of *Potamogeton amplifolius* and *P. robbinsii* remained stable year-round and showed minimal seasonal fluctuation. *Potamogeton amplifolius* typically did not fruit when growing at a depth of 3 m or more, and densities from one to ten plants per square meter were found at this depth. In shallow water this species fruited, and in the autumn the dieback in the shallow lake periphery was readily observed. Annual densities of *P. robbinsii* varied from 100 to 1000 plants per square meter at depths from 5 to 7 m.

To confirm that the vegetative plants found during the winter continued to be metabolically active, we removed plants in midwinter and compared photosynthetic rates (3) to those of plants from midsummer (Table 1). Plants gathered during the winter exhibited 10 to 20 percent the photosynthetic activity of summer rates. On a clear winter day with minimal snow cover on top of the ice, approximately 4300 lux (light intensity) penetrated to 5 m. Light saturation for photosynthesis by two species, *P. robbinsii* and *P. amplifolius*, was approximately 2300 lux. For *P. robbinsii*, at densities found in Smith Bay at 5 m, maximum midday productivity during the winter ranged from 1.65 to 16.5 mg of carbon fixed per square meter per hour as compared to summer productivity rates, which ranged from 13.2 to 132 mg of carbon fixed per square meter per hour. *Potamogeton amplifolius* exhibited a maximum midday winter productivity at 3 m from 0.27 to 2.68 mg of carbon fixed per square meter per hour as compared to a summer maximum of 4.82 to 48.2 mg of carbon fixed per square meter per hour.

Aquatic macrophytes are an important ecological and limnological component of the aquatic ecosystem (1). Their role

in summer productivity and contribution to the annual recycling of nutrients is well established (4). The omission of references to winter growth of submergent macrophytes in recent books on macrophyte productivity (5) suggests that there is relatively little known about growth under ice cover. The best data are those of Rich *et al.* (6), who report that *Scirpus subterminalis* maintains substantial viable biomass throughout the winter under ice cover. Rich *et al.* found that the submersed annual macrophytes of Lawrence Lake, represented mainly by *Potamogeton illinoensis* and *P. praelongus*, die back in the fall. In Lake George many species, including *P. praelongus*, when growing at depths of 3 m or more, maintain high viable biomass.

Karyotypic Analysis and Evidence of Tetraploidy in the North American Paddlefish, *Polyodon spathula*

Abstract. A modal chromosome number of 120 was obtained for the ancient fish, *Polyodon spathula* (Pisces: Chondrostei). The karyotype consists of 48 macrochromosomes and 72 microchromosomes. The microchromosomes are like those found in certain other primitive fishes as well as in reptiles and birds. The possibility that *Polyodon* is a species of tetraploid origin is strongly suggested by the fact that the 120 chromosomes are easily arranged into 30 groups of four homologs each. Evolutionary comparisons are made with other primitive fish groups.

The most ancient living ray-finned fishes, subclass Actinopterygii, belong to the superorder Chondrostei which includes the paddlefishes, family Polyodontidae, and the sturgeons, family Acipenseridae. Representative polyodontids are found in fossil deposits ranging from the Upper Cretaceous to Recent. Evidence indicates that they evolved from the extinct palaeoniscid fishes of the Pennsylvanian to Cretaceous (1). The fossil record also indicates that these

Continued winter growth of aquatic annuals in temperate climates is probably considerably more common than had been thought.

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References and Notes

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2. Plant densities for each species were approximated in situ with the use of an exponential scale encompassing a range from 0.001 to 5000 plants per square meter (R. B. Sheldon and C. W. Boylen, manuscript in preparation).
3. Photosynthetic rates were determined by incubating washed apical portions for 2 hours in filtered lake water in the presence of 1 μ C of $\text{NaH}^{14}\text{CO}_3$ (specific activity, 100 μ C per milligram of NaHCO_3 ; New England Nuclear, Boston). Illumination was controlled by rheostat to 22,000 lux. Dried leaf material was digested in 1N NaOH for 30 minutes at 100°C, and after neutralization with 1N HCl, further fragmented in a glass homogenizer. Portions were examined for radioactivity (Beckman scintillation counter model LS-133). Photosynthetic rates are expressed as milligrams of carbon fixed per hour per milligram of dry weight.
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7. Supported by the Eastern Deciduous Forest Biome, United States-International Biological Program, funded by the National Science Foundation under interagency agreement AG-199, BMS 69-01147 A09, with the Energy Research and Development Administration-Oak Ridge National Laboratory, Contribution No. 262 from the Eastern Deciduous Forest Biome, US-IBP.

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chondrosteian ancestors were eventually replaced by the better adapted holostean fishes, represented today only by the relict gars and bowfin. Finally, the holosteans themselves were replaced by the superior teleostean fishes which swarm the freshwaters and oceans of today and number approximately 30,000 species.

From an evolutionary viewpoint, it is of interest to determine the chromosome number and morphology of the extant chondrosteans. One species of sturgeon,