The Biology of Aquatic Plants

P. B. Tomlinson

Asa Gray in his study of the genus *Potamogeton* (the pondweeds) referred to them as a "set of vile little weeds." Although this largely was with reference to their taxonomic complexity, it might well have reflected common attitudes in the 19th century towards plants of wetlands. Aquatic plants, with few exceptions, would have appeared to have neither commercial nor aesthetic value, and a study of them, except by the most devoted specialist, certainly might have been something of a chore. The situation is much different today because of the increasing awareness of the mutual dependence among organisms and a greater appreciation for the role that plants play in maintaining and stabilizing living communities. Wetlands are now known to be centers of initiation for complex food chains, and they play a part in the natural regulation of water resources. The heightened appreciation among professional biologists and amateur naturalists for the biological diversity that wetlands exhibit and the examples they can provide of adaptive processes is matched by an increased appreciation for aquatic plants as horticultural subjects. This comes from the very features that earlier had led to their neglect: the naturalism they can lend to cultivated landscapes. Part of this attraction is the multiplicity of forms characteristic of aquatic plants. Some of this variation occurs within single species and is one of the features that make them difficult to categorize taxonomically. This structural plasticity often helps a species adapt to an aquatic environment. Because water levels fluctuate, the adaptive response of the plant often must change.

Without seeking more academic clarification, one can accept the terms "aquatic plant" and "wetland" as describing, respectively, plants that have some association with an environment with superabundant water and the vegetation type itself. This habitat may range from open water to regions with a seasonally water-logged soil; the water may be still or flowing. In the more typical situation, aquatic plants may grow in, on, or under water, the form of the plant frequently being highly adjusted to each situation. Free-floating plants have only a limited root system; submerged plants often have slender or trailing leaves.

Based on north temperate experience, "aquatic plant" implies herbaceous plants but should include woody plants like alders, willows, and sweet gale, even though these may show no conspicuous adaptation to the wetland environment. However, in the shrubby genus *Decodon,* for example, the stems spread over the surface of the water and are modified so that they will initially float without getting water-logged. Unfortunately, most manuals of aquatic plants exclude a consideration of woody species. This restriction is particularly inappropriate in the tropics, where swamp forests of considerable diversity exist, with the trees developing modified root systems in order to adapt to water-logged soils. Mangroves, or tidal forests, represent the most specialized group of woody aquatic plants, which are adapted to regular tidal inundation and demonstrate remarkable strategies that allow them to grow in the sea. Such is the dominance of trees in these tidal forests that the latter contain virtually no herbaceous plants.

Another extreme marine community is provided by the so-called "seagrasses," that is, flowering plants that live in the sea and always remain submerged except at the lowest tides. The word *seagrass* is a misnomer. Although the plants are all monocotyledons they are not related to the true grasses (family Gramineae or Poaceae). Their closest relatives are, in fact, the pondweeds and water-plantains of freshwater communities. Seagrasses can form extensive marine meadows in both tropical and temperate regions, almost invariably in sedimentary deposits that the larger seaweeds do not colonize well. *Zostera* (eelgrass) is the most familiar example in the northeastern United States. Seagrass communities are recognized as primary producers and stabilizers, providing directly or indirectly nutrients and shelter for a variety of marine-animal life. Their ecological importance, however, was recognized only quite recently.

The study of both mangrove and seagrass communities has excited much attention among scientists because these plants epitomize the ideal agricultural or forestry system: they are self-fertilizing, self-irrigating, and self-generating, since their constituent species have remarkable adaptations for establishment. They represent an entrepreneur's dream, since they produce, on a renewable basis, raw materials from seawater!

In the familiar freshwater herbaceous plants the biologist sees clear examples of structural modifications that adapt the plants to the varying degrees of wetness of the habitat. Submerged plants have pliable linear or dissected leaves, which minimizes drag resistance to moving water currents. The tissues are light and air-filled so that the organs are both bouyant and permit a certain development of an internal atmosphere. Mechanisms also exist for appreciable internal mass movement of gases: "internal winds" that facilitate oxygenation of root systems via floating leaves have been observed in water-lilies. In the more specialized aquatics mechanical tissues are reduced, since their erect organs are largely supported by the bouyant medium. Consequently, they have surplus biomass for extension and this accounts for their relative profligacy. "Water weeds" seems an appropriate term for plants that can rapidly block canals and ponds and generally create a nuisance where free passage is desired.

One must always, however, interpret the functional significance of structural modifications with care. Aquatic plants typically have reduced water-conducting tissue (xylem), presumably because they are able to absorb over the whole of their surface that is in contact with water. Conserving internal water and minimizing its loss is not a problem for them. This does not necessarily mean that the xylem is totally nonfunctional, even though the cells are thin-walled. There is some evidence for a transpiration stream, as in terrestrial plants, but functioning with the minimal risk of internal collapse of the conducting pathway. Sometimes, therefore, the probable water-conduits are internal canals from which normal thick-walled xylem cells disappear early in development.

Specialization of the reproductive organs varies in aquatic plants. Most specialized aquatics have water-dispersed seeds (or spores), efficient because the seed largely remains within the medium appropriate for establishment. In most aquatic flowering plants the flowers are developed aerially and show no specialization relevant to the habitat. The flowers of *Utricularia* (the bladderworts) contrast remarkably with the vegetative parts, for example. In some aquatics, however, pollination occurs at or below the water surface and the modification always involves simplification of parts. Consequently, ancestral forms are not easy to trace. However, pollination at the water surface is particularly efficient; since pollen moves in only two dimensions the "target" (stigma of another flower) is easier to find than in three-dimensional submerged pollination. To facilitate attachment of pollen to stigmas in a number of plants whose life cycle is completed entirely under water, the pollen grains are individually threadlike or filamentous, as in eelgrass, or adhere in long chains, as in turtle-grass (*Thalassia*). A floral mechanism in which the pollen gets wet offers considerable physiological problems compared with the normal method of dispersal of dry pollen. The water-soluble protein material that accompanies the pollen in normal aerial pollination, and which is part of the cell-recognition system of the pollen-stigma interaction, is dispersed and no longer effective in underwater pollination. We do not, in fact, know how this recognition system works in submerged flowers, although the cell surface of pollen that germinates in submerged stigmas usually lacks the specialized wall layers that in dry pollen retain the protein recognition component. This reference to the change from ancestral aerial pollination to derived submerged pollination is but one example of evolutionary modification in plants of aquatic environments.

Studies of the biology of aquatic plants are numerous because of the diversity of functional mechanisms that the plants display. A number of excellent summaries provide the necessary overview. The earliest compendia were produced by German authors, and the work of Schenck is noteworthy. The English botanist Agnes Arber provided the first treatise in English, and the book has become a classic, as much for the limpid style as for the scientific content. More recent summaries include a very comprehensive survey by Sculthorpe. Shirley Haslam has provided an ecological description of river plants. At the taxonomic level there are treatments of aquatic and wetland plants of several areas of the United States, and I myself have dealt with the seagrasses in a volume that places them in their systematic context. The list lengthens as one contemplates the contemporary scene; the flow of scientific literature guarantees that bookshelves will be filled.

In addition to these books I have listed below a few examples of more readable scientific papers that elaborate on some of the points I have dealt with. I think that if Asa Gray were around today he would have cause to change his opinion about "waterweeds." They offer remarkable examples of evolutionary modification in relation to the demands of a diversity of habitats that may be subject to continual change.

Representative Publications on Water Plants

BOOKS

Arber, A. 1920. *Water Plants: A Study of Aquatic Angiosperms* Cambridge University Press, Cambridge, England. A classic account, marked by a lucid and distinctive expository style. It was reprinted in 1963 as a measure of its importance and still serves as a guide for the older literature.

Cook, C. D. K., B. J. Gut, E. M. Rix, J Schneller, and M. Leitz. 1974. *Water Plants of the World.* W. Junk. The Hague A manual for the identification of the genera of freshwater macrophytes. A comprehensive systematic overview of aquatic plants on a cosmopolitan basis.

Correll, D. S., and H. B. Correll. 1975. *Aquatic and Wetland Plants of the Southwestern United States* (2 vols.). Stanford University Press, Stanford A detailed systematic treatment of plants in this geographic area.

Godfrey, R. K., and J. W. Wooten 1979. *Aquatic and Wetland Plants of the Southeastern United States* Monocotyledons. University of Georgia Press, Athens, Georgia. A systematic treatment of a geographical area.

Haslam, S. M. 1978. *River Plants The Macrophytic Vegetation of Water Courses* Cambridge University Press, Cambridge, England. A description of plants in flowing waters, largely with examples from English rivers

Magee, D. W. 1981. *Freshwater Wetlands: A Guide to Common Indicator Plants of the Northeast.* University of Massachusetts Press, Amherst, Massachusetts. A popular illustrated account with identification keys and descriptions of plants and habitat.

Mason, H. L. 1957 *A Flora of the Marshes of California* University of California Press, Berkeley, California. A regional flora of wetland plants.

Schenck, H 1886 *Die Biologie der Wassergewachse.* Max Cohen, Berlin. An early review (in German) that established basic structural features of aquatic plants.

Sculthorpe, C. D. 1967. *The Biology of Aquatic Vascular Plants.* Edward Arnold, London. A comprehensive survey but now a little out of date.

Tomlinson, P. B. 1982. Helobiae (Alismatidae). Vol. 7 in *Anatomy of the Monocotyledons* C. R. Metcalfe, ed. Clarendon Press, Oxford. A technical description on a systematic basis of the group that includes all the seagrasses and the more exclusively aquatic families of monocotyledons.

SPECIALIZED PAPERS

Cook, C. D. K. 1982. Pollination mechanisms in the Hydrocharitaceae. Pp. 1–15 in *Studies on Aquatic Vascular Plants* (J. J Symoens, S S. Hooper, and P. Compère, eds.). Royal Botanical Society of Belgium, Brussels. A fascinating account of the diversity of pollination mechanisms that can occur in an aquatic family.

Dacey, J. W. H. 1981. Pressurized ventilation in the yellow waterlily. *Ecology* 62: 1137–47. An account of how differential pressures are generated and can create "internal winds" that promote gas exchange in an aquatic plant.

Ogden, E. C. 1974. Anatomical patterns of some aquatic vascular plants of New York. New York State Museum Scientific Service Bulletin 424. A detailed description of anatomical features, often important in identification.

Pettitt, J., S. Ducker, and R. B. Knox. 1981. Submarine pollination. The sea grasses, flowering below the ocean surface, must shed and capture pollen in an underwater habitat. What are the differences between their system of reproduction and that of land-based plants? *Scientific American* 244: 135–143.

P B Tomlinson is a professor of biology at Harvard University. He is currently working on a book about mangroves.