Macrophytes:

*Where They Grow and Why**

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Macrophytes (large plants) are aquatic plants we can easily see with the "naked" eye. They consist principally of aquatic vascular flowering plants, but they also include some aquatic moss, liverwort, fern, large algae, and non-flowering vascular plant species. They all inhabit the littoral zone—that area of a lake where plants grow. This is the easy answer to where macrophytes grow. The detail is in why the littoral zone is the ideal area for plant growth.

Most macrophytes are secondarily adapted to life in the water. They once lived on land and gradually evolved mechanisms to deal with a watery world. But their needs evolved differently, so different types of plants need different combinations of sediment, air, and water to thrive.

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Different kinds, or life forms, of plants dominate different areas of the littoral zone. Emergent plants like cattails and bulrushes are most common in shallow water (1 to 2 m deep). These species are rooted in the bottom sediment, grow through the water, and develop strong supportive tissue to reach into the air for needed sunlight and carbon dioxide. In slightly deeper water, floating-leaf species like water-lilies and lotus dominate. They can get needed sunlight and carbon dioxide from the air, but they do not build strong supporting tissue to reach skyward. They depend on buoyancy to keep their leaves afloat. Only submersed species are found in deep areas of the littoral zone. They grow entirely underwater, although some species may flower above water or produce single floating leaves. They get needed carbon dioxide from the water and needed sunlight is filtered through the water. Although submersed species can be found in the deepest area of the littoral zone, some submersed species are found in very shallow water. The above groups are rooted and probably get the majority of their nutrients from sediment. Another group, like the duckweeds and water hyacinth, is free-floating. They are not anchored in the bottom and most float at the water surface. They get vital materials from the water and air. Wind, waves, and current may determine where they are found.

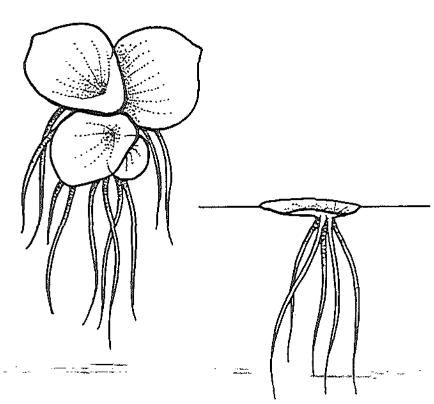
Scales of Plant Distribution

Where plants grow will be discussed on two scales—the within-lake scale and the between-lake or regional scale. Why do plants grow in certain areas of a lake and not in others? Why do some plants grow in lakes of southern Wisconsin and not northern Wisconsin or in Florida lakes and not Vermont lakes?

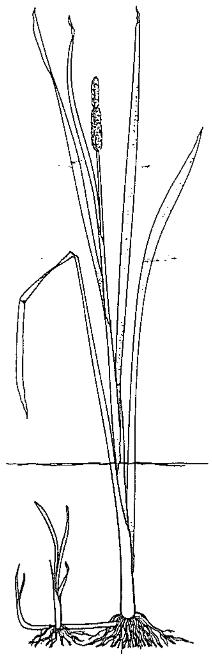
The most important environmental factors affecting the abundance and distribution of macrophytes within lakes are light availability, sediment characteristics including nutrients, and wind and wave energy. Lake morphology, size, and watershed characteristics are related to these factors. Water chemistry, nutrient status, and temperature are important factors determining plant distribution between lakes or on a regional scale. Another factor is dispersal. A plant might be able to grow under a wide variety of conditions, but if it has not been transported to a suitable location, it will not be found there.

Within-Lakes

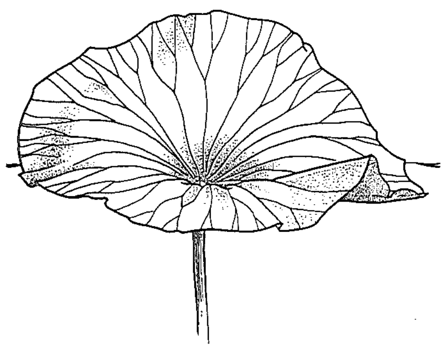
Light availability. Aquatic plants require light for growth; thus, light availability is the most crucial environmental factor regulating the maximum depth of plant growth. Light availability is directly linked to water



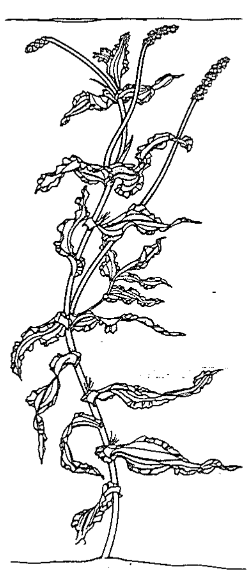
Great duckweed—an example of a free-floating species. Free-floating species get vital materials from the water and air. Wind, waves, and current usually determine where they are found.



Broad-leaf cattail—an example of an emergent species. Emergent species are rooted in bottom sediments, grow through the water column, and have strong supportive tissue to hold them upright in the air.



American lotus—an example of a floating-leaf plant. The "stem" in some floating-leaf plants is actually a leaf petiole that connects to a rhizome (underground stem). Although floating-leaf species are not as subject to the whims of wind and current as free floating species, they are usually found in quiet water. They do not have strong supportive tissue like emergents, so they get torn at exposed sites.



Clasping-leaf pondweed—an example of a submersed species. Submersed species are rooted in sediment and live completely underwater. Light attenuation and slow CO_2 diffusion are two limitations of this habitat.

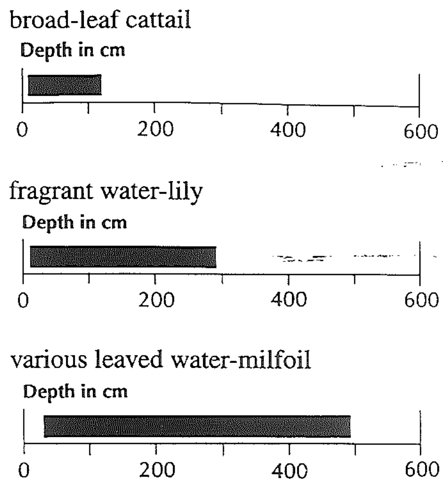
clarity. As water depth increases or water clarity decreases, the amount and the spectral quality of light for photosynthesis at the lake bottom diminishes. Generally, submersed macrophytes will grow to a depth of two to three times the Secchi depth (depth at which a black-and-white disk lowered into a lake disappears). Thus, lakes with the majority of their bottom exceeding two to three times the Secchi depth will have fewer aquatic macrophytes. Even shallow lakes, if they are turbid, will have sparse submersed aquatic plant growth.

Water clarity in most lakes is controlled by phytoplankton, organic color, and organic and inorganic suspended particles. Lakes with low phytoplankton concentrations and low color values have high water clarity. As phytoplankton and color levels increase, there is a rapid reduction in water clarity, submersed macrophytes become light limited, and the size of the littoral zone decreases. Conversely, the size of the littoral zone can increase if phytoplankton or color levels decrease, which can occur where management efforts reduce nutrient levels in a lake.

The amount of non-algal suspended particles (suspended solids) in a lake is determined by the continuous process of tributary input, sedimentation, and resuspension. Shallow lakes that have substantial layers of soft sediments and are open to the wind may have high suspended solids concentrations due to wind mixing of bottom sediments. Suspended solids limit light for plant growth and decrease littoral zone size. Boat traffic, shoreline erosion, and biotic factors like common carp can also increase suspended sediment.

Sediment characteristics. Bottom sediments can act as a nutrient source and an anchoring point for aquatic plants. However, some bottom types (e.g., rocks or cobble) are so hard that plant roots cannot penetrate them; others are so soft, flocculent, and unstable that they will not anchor plants. Extremely coarse-textured sediment (sand) can be so nutritionally poor for macrophyte growth that small accumulations of organic matter stimulate plant growth.

Anaerobic (no oxygen) conditions found in some lake sediments may have a profound effect on plant growth. Low dissolved oxygen concentrations, or high concentrations of soluble reduced iron and manganese or soluble sulfides, can be toxic to plants. High soluble iron concentrations interfere with sulfur metabolism and limit the availability of phosphorus. Sediments containing excessive organic matter may contain high concentrations of organic acids, methane, ethylene, phenols, and alcohols that can also be toxic to vegetation. The above conditions are most frequently found in anaerobic sediments of eutrophic (nutrient rich) or hypereutrophic (very nutrient rich) lakes. To some degree, aquatic plants can protect themselves from these toxins with oxygen released from roots, which eliminates the anaerobic conditions that create the toxic substances.



Comparison of depth distributions of broad-leaf cattail, an emergent species, with fragrant water-lily, a floating-leaf species, and various-leaved water-milfoil, a submersed species in Wisconsin lakes.

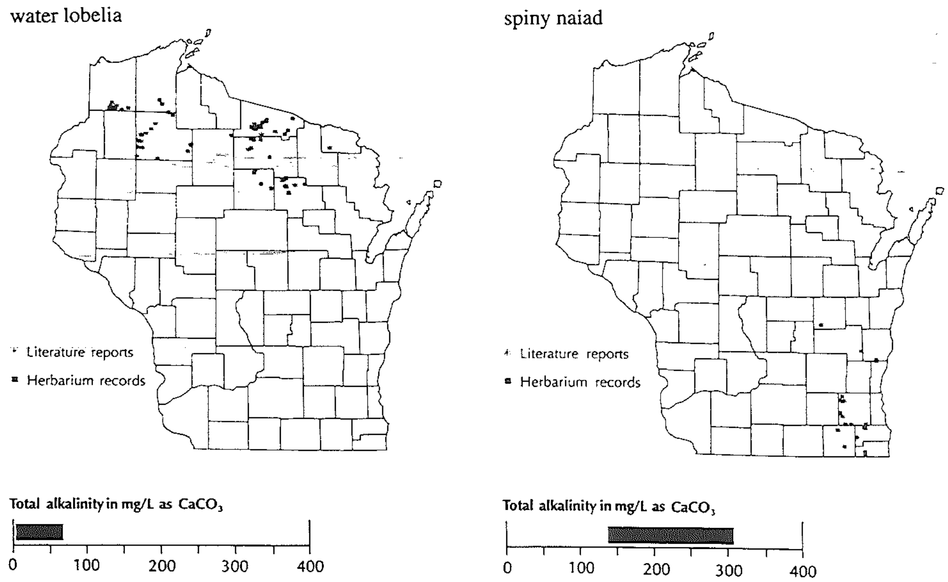
Plant nutrition. Submersed macrophytes use aqueous and sedimentary nutrient sources, and sites of uptake (roots vs. shoots) are related, at least in part, to nutrient availability in sediment versus the overlying water. In other words, submersed plants are operating like good opportunistic species should operate; they take nutrient supplies from the most available source.

Rooted macrophytes usually fulfill their phosphorus (P) and nitrogen (N) requirements by direct uptake from sediments. The role of sediment as a source of P and N for submersed macrophytes is ecologically quite significant because available forms of these elements are normally in very low concentrations in open water during the growing season. Likewise, the availability of micronutrients in open water is usually very low, but they are relatively available in most sediments. However, the preferred source of some nutrients such as potassium (K), calcium (Ca), magnesium (Mg), sulfate (SO_4), sodium (Na), and chloride (Cl) appears to be the open water. Free-floating species have to obtain their nutrients from the water column and may directly compete with algae for available nutrients.

There are few substantiated reports of nutrient-related growth limitation for aquatic plants. Nutrients supplied from sediments combined with those in solution are generally adequate to meet nutritional demands of rooted aquatic plants, even in oligotrophic (nutrient poor) systems. Although this information suggests that nutrients do not limit growth of aquatic plants in oligotrophic lakes, these lakes generally maintain less total biomass of aquatic plants and usually contain different species than eutrophic lakes.

Lake morphology—an integrating factor. Turbidity, nutrient concentration, sediment texture, sediment organic matter, siltation rates, and wind and wave action are important factors determining aquatic plant distribution and abundance. These parameters are interrelated and interact with basin depth, bottom slope, surface area, and shape to determine littoral zone size.

Lake basins are extremely variable—they reflect the water body's origin and they are constantly being modified by water movements within the basin and sediment inputs from the watershed. As basins are modified, the size of the littoral zone in relation to the lake's open water changes; most water bodies become shallower. Unless something or someone intervenes, littoral zone size increases as a water body gets older.



Comparison of the distribution of water lobelia with spiny naiad in Wisconsin lakes. Spiny naiad is found only in high alkalinity lakes of southeastern Wisconsin. Water lobelia is found only in low alkalinity lakes of northern Wisconsin. Many species found in low alkalinity lakes are "isoetid" type plants and have special mechanisms for obtaining carbon from low carbon environments.

Water depth is one of the most critical environmental factors determining the lakeward extent of the littoral zone. With some exceptions, a depth range between 9 and 14 meters is the limit for most aquatic plants and the maximum depth of plant growth in many lakes is much shallower. Emergent and floating-leaved plants seldom grow in water exceeding 3 meters, so deep lakes also have limited emergent communities.

The steepness of the littoral slope is inversely related to the maximum biomass of submersed macrophytes. Probably this is due to the difference in sediment stability on gentle and steep slopes. A gentle sloping littoral allows the deposition of fine sediments that promote plant growth. Steeply sloped littorals are areas of erosion and sediment transport, areas not suitable for plant growth. The manipulation of lake depth and slope are powerful management tools when encouraging or discouraging the growth of aquatic plant in specific areas of a lake.

All lakes have a shoreline-water interface that receives energy from wind and waves. Surface area and shape significantly influence the effect wind has on wave size and current strength. Large lakes tend to have larger fetches (area open to the prevailing wind) and thus have greater wave and current energy than lakes with small surface areas. Wave action and currents erode a terrace along the shoreline, leaving coarse material in shallow water and depositing fine materials in deep water. The direction and strength of the wind, slope, and shape of the lake basin determine where the substrates will move. Generally, points and shallows where wind and wave energy are highest are swept clean. Bays and deep spots in a lake fill with sediment. The quantity and quality of silt in shallow water may control the distribution of submersed vegetation. Large lakes with many bays or coves may develop an extensive littoral zone because these areas are protected from strong waves and currents. Thus, basin size, shape, and depth determine the distribution of sediments in a lake and therefore the distribution of aquatic plants.

Regional Distributions

Water chemistry. All things being equal, nutrient-poor lakes are less productive than nutrient-rich lakes. A primary factor determining the trophic status (nutrient richness) of a lake is the geologic region where the lake occurs. Watershed-management practices and direct human-caused nutrient additions can also be important.

Inorganic carbon is the nutrient most likely limiting submersed macrophyte photosynthesis. The difficulty plants have in carbon dioxide (CO_2) transport is known to limit photosynthesis in terrestrial plants and is even more critical in submersed species because the diffusion of CO_2 is much slower in water than in air. Free CO_2 is the more readily used carbon form for photosynthesis. Some species can utilize bicarbonate as a carbon source, but they do so less efficiently. The ability to use bicarbonate has adaptive significance in many freshwater systems because the largest fraction of inorganic carbon may exist as bicarbonate. The ratio of CO_2 to bicarbonate to carbonate is determined by the alkalinity and pH of the water. Alkalinity and pH vary regionally or at least between lakes and influence the species composition in lakes over broad geographic regions. Of course, this water chemistry relationship probably doesn't influence the distribution of species, like emergents, that rely on the atmosphere for their carbon supply.

Water temperature. Water temperature is another factor that controls plant distributions over broad geographical areas. In Wisconsin, for example, we don't worry about some aquatic nuisance species like water hyacinth. Freezing temperatures negate any problems on an annual basis. There are some species that are cold-water strategists; they have a competitive advantage because they can photosynthesize better in cold water temperatures than other species so they can grow earlier in the spring and grow longer in the fall. Some exotic nuisance species like Eurasian water-milfoil are physiologically adapted to compete well over broad geographical ranges. It can photosynthesize better at lower water temperatures and utilize bicarbonate for photosynthesis better than many native species.

Dispersal. Another reason an aquatic species is not in a particular location may be that it has not gotten there. We do not know a lot about aquatic plant dispersal under natural conditions but it is a case of reverse island biogeography. That is, lakes are islands in a "sea" of land that is difficult for aquatic plants to cross. We do know that with better access to lakes and with more people using lakes that long-distance dispersal of aquatic plants by people, usually inadvertently, is a growing concern, especially for the transport of nuisance species.

Hydrilla, for example, is an exotic nuisance that appears to be able to survive in northerly climates. The reason it is not yet a problem in Wisconsin may just be that it has not arrived and successfully established itself.

Summary

Large/small, deep/shallow, acid/alkaline, oligotrophic/eutrophic, warm/cold, hard bottom/soft bottom—there is tremendous variety in the waters of the world, but usually there are plants than can live there. The main differences are what kind, where, and how many. Large, cold, deep, nutrient-poor systems generally have less biomass and less of the lake volume where aquatic plants grow. However, they can still have a substantial percentage of the lake area with plant cover. Shallow, warm, nutrient-rich systems have the potential to produce large biomasses of aquatic plants. However, this potential is not always reached because of heavy phytoplankton growth, turbidity, or soft, anoxic sediments. This article only discussed major factors that influence macrophyte growth and distribution. Aquatic plants also modify the littoral zone habitat and the whole lake ecosystem, but that is material for another article.

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