

Evolution of Aquatic Angiosperm Reproductive Systems

What is the balance between sexual and asexual reproduction in aquatic angiosperms?

C. Thomas Philbrick and Donald H. Les

As angiosperms diversified and flourished in terrestrial habitats, some species ultimately colonized freshwater or marine environments and became aquatic. Aquatic plants are species that perpetuate their life cycle in still or flowing water, or on inundated or noninundated hydric soils. Aquatic angiosperms inhabit oceans, lakes, rivers, and wetlands.

The transition to an aquatic life has been achieved by only 2% of the approximately 350,000 angiosperm species (Cook 1990). Nonetheless, the evolutionary invasion of aquatic environments by terrestrial angiosperms is estimated to represent 50–100 independent events (Cook 1990). Although aquatic plants are typically discussed as a unified biological group, the ways that species have evolved to life in the aquatic milieu are as diverse as the different evolutionary lineages that became aquatic (Hutchinson 1975, Sculthorpe 1967). Reproductive and other life-history traits of aquatic angiosperms are closely associated

Aquatic plants are an extremely heterogeneous assemblage of species that survive in similar habitats but as a result of fundamentally different evolutionary pathways

with specific growth forms: emersed from the water, free-floating, floating-leaved, or submersed. These categories represent different degrees of adaptation to aquatic life and are widely convergent among aquatic angiosperms.

As in terrestrial plants, reproduction in water plants consists of both sexual and asexual mechanisms. Sexual reproduction (the chief source of hereditary variation via genetic recombination) in plants is considered to be advantageous in changing or heterogeneous environments, and asexual reproduction (which perpetuates genetic uniformity) is considered to be more successful in stable or uniform habitats (Grant 1981, Williams 1975). Consequently, the evolution of aquatic plant reproductive systems should reflect the relative stability of their habitats.

A vast assortment of freshwater and marine environments exists. Nevertheless, aquatic habitats tend to be stable (Hartog 1970, Sculthorpe 1967, Tiffney 1981). Water exhibits

greater chemical and thermal stability than air, and it buffers against (or even precludes) many types of catastrophic disturbance that plague terrestrial habitats, such as rapid temperature changes, fires, floods, and strong winds. At higher latitudes, seasonal stability of aquatic habitats is faithfully maintained by the density of water, which is greatest (depending on salinity) at approximately 4°C (Wetzel 1975). Thus, even in the coldest temperatures, lake and river bottoms typically remain ice free.

Coastline and freshwater shore aquatic habitats have been viewed as inherently unstable (Laushman 1993) due to erosional processes, tidal fluctuations, and wave dynamics. However, habitat stability should be evaluated not only in terms of characteristic short-term variation, but also over the course of longer, evolutionarily significant time frames. In this sense, stability reflects the consistent expression of predictable habitat characteristics over long time periods. In essence, aquatic habitats may be quite variable, yet vary in a similar, predictable fashion through time. The angiosperm family Podostemaceae (riverweeds) illustrates this concept well. Riverweeds grow tenaciously attached to rocks in tropical river rapids and waterfalls. Although the rushing current makes this habitat unstable ecologically, the seasonally high and low water levels make it a predictable habitat in which riverweeds flourish (Philbrick and Novelo 1995).

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No aquatic habitat is absolutely stable. Factors such as continental drift have lead to drastic ecological changes in coastal marine environments. Cultural eutrophication and pollution can rapidly alter the trophic status of aquatic habitats. The sporadic outbreak of pathogens, such as the agent responsible for the devastating wasting disease of the seagrass *Zostera marina* (Zosteraceae; Muchlstein et al. 1991), is yet another aspect of instability in aquatic environments.

In evolutionary time frames, aquatic habitats represent a mosaic of both stable and unstable conditions to which complex adaptation has been necessary. Recalling the paradigm for the evolution of asexual and sexual reproductive systems, it is evident that both systems should retain important functions in the majority of water plant species. In this article, we discuss possible evolutionary factors to account for the balance between sexual and asexual reproduction that is maintained in aquatic angiosperms.

Asexual reproduction

Asexual reproduction includes both seed production without fertilization (agamospermy) and vegetative reproduction. Because the extent of agamospermy among aquatic plants is poorly understood (Les 1988a), we limit our discussion to vegetative reproduction, which is often assumed to be the dominant mode of reproduction in water plants (Hutchinson 1975, Sculthorpe 1967). Abrahamson (1980) considered that genetically identical offspring render the process of vegetative reproduction more similar to growth (increase in size of an individual) than to reproduction (increase in the number of individuals). However, ramets (veg-

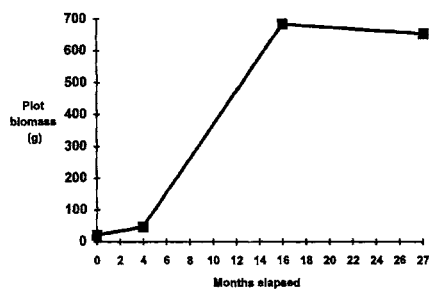


Figure 1. Asexual reproduction in aquatic plants occurs rapidly. Biomass (grams of dry weight) measured in 2 m × 2 m field plots planted initially with 100 small fragments of Eurasian water milfoil (*Myriophyllum spicatum*). Within 16 months, vegetative growth had reached maximum biomass levels (carrying capacity). Biomass had more than doubled during the first four-month growing season (from Les et al. 1988).

etatively produced progeny) are not always identical genetically to the parent (see below). In any case, they represent a legitimate example of reproduction in which discrete, new individuals are produced and dispersed.

Asexual reproduction is important in the establishment, growth, and maintenance of aquatic plant populations. For example, in weedy aquatic plants, most emergent species disperse by sexual propagules, whereas floating and submersed species disperse vegetatively (Cook 1993, Spencer and Bowes 1993). Nevertheless, the principal means of population increase for all three growth forms is by vegetative reproduction (Spencer and Bowes 1993). Certainly, the ease and rapidity by which aquatic weeds spread throughout nonindigenous regions attests to the efficiency of vegetative reproduction.

Nuisance aquatic weeds such as water hyacinth (*Eichhornia crassipes*, Pontederiaceae) and Eurasian water

milfoil (*Myriophyllum spicatum*, Haloragaceae) have spread over vast areas by asexual means. Field studies (Les 1990) indicate that plots planted with small fragments of water milfoil can reach carrying capacity in only 16 months (Figure 1). Such results express the futility of control efforts if aquatic weed introductions are not recognized, and plants eradicated, immediately after initial colonization.

Most aquatic plants are not troublesome but possess mechanisms for asexual reproduction similar to those of their weedy counterparts. Many common names such as waterweed, pondweed, and riverweed are unwarranted but have probably originated because of the tendency for water plants to grow in luxuriant beds formed by vigorous vegetative growth. Some native aquatic plants are actually more productive than introduced weedy species but have a less effective vegetative growth architecture. For example, experiments in which vegetative fragments from both a native pondweed and introduced milfoil species were planted simultaneously show greater biomass productivity in the native species (Table 1; Les et al. 1988). Additional experiments have further indicated no evidence of competition between these species under normal environmental conditions (Les et al. 1988). Elevated nutrients resulted in the accelerated growth of both species (Les 1990), but milfoil biomass was mostly allocated to produce long, vertical shoots, whereas much pondweed biomass was allocated to horizontal rhizomes (Table 1). Rapid vertical growth under enhanced nutrient regimes enables milfoil to quickly grow to the water surface, where it shades native plants, indirectly causing their decline.

The ability to reproduce vegeta-

Table 1. One season of vegetative growth compared between a native pondweed (*Potamogeton amplifolius*) and the nonindigenous Eurasian water milfoil (*Myriophyllum spicatum*) planted experimentally in a Wisconsin lake (from Les et al. 1988). Data are expressed as means; NA = not applicable (*Myriophyllum* does not produce rhizomes). The original shoot cuttings of *Potamogeton* lacked rhizome tissue.

Species	Shoot biomass (g)		Shoot length (cm)		Rhizome length (cm)		Leaf number	
	Initial	Final	Initial	Final	Initial	Final	Initial	Final
<i>Potamogeton amplifolius</i>	0.25	1.18	3.2	50.0	0.0	47.5	4	52
<i>Myriophyllum spicatum</i>	0.20	0.88	15.0	190.0	NA	NA	39	490

tively is ubiquitous among aquatic species, regardless of their taxonomic affiliation (Grace 1993, Hutchinson 1975, Les and Philbrick 1993, Sculthorpe 1967). However, aquatic plants are more common proportionally in monocots than dicots (Les and Schneider 1995). Tiffney and Niklas (1985) postulated that the greater proportion of aquatic monocots is associated with the high incidence of rhizomatous growth (i.e., by horizontal underground stems) in monocots. In contrast, far fewer dicots are rhizomatous (Grace 1993). This correlation suggests that clonal growth is conducive to the evolution of aquatic species.

Although annuals (in which reproduction is exclusively sexual) and perennials are relatively evenly distributed among terrestrial plant groups, most aquatic plants are perennial. Perennial water plants possess many contrivances for vegetative reproduction (Figure 2), including corms, rhizomes, stolons, tubers, and turions (Grace 1993, Hutchinson 1975, Sculthorpe 1967, Vierssen 1993). Even the few predominantly annual aquatic plant genera such as *Najas* (Najadaceae) may reproduce vegetatively during the growing season by extensive lateral growth, fragmentation, or the occasional production of turions (Agami et al. 1986, Sculthorpe 1967).

Asexual reproduction is also common among terrestrial plants, and the transport of tubers, corms, and small bulbs confers high potential vagility (ability to disperse) to perennial angiosperms (Stebbins 1950). Water plants excel in this capacity with a variety of vegetative structures that are highly specialized to function efficiently as propagules, some even capable of long-distance dispersal. Vegetative propagules are important agents of gene flow in aquatic plants (Barrett et al. 1993, Les 1991). The highly vagile propagules of aquatic plants are exceptions to the generalization (Williams 1975) that asexual offspring develop close to the parent, as opposed to sexual offspring, which are more widely dispersed.

The most notable vegetative propagule in aquatic plants is the turion (Figure 2b), a specialized structure with few functional coun-



Figure 2. Aquatic plants employ many types of vegetative structures for reproduction. (a) Modified horizontal stems (rhizomes) grow quickly to anchor aquatic plants in unconsolidated, shifting substrates. This specimen of pondweed (*Potamogeton amplifolius*) resulted from the planting of a small four-leaved fragment that initially lacked a rhizome. The growth illustrated here occurred during a single summer season. (b) Highly specialized vegetative leaves help to insulate this spherical turion of bladderwort (*Utricularia vulgaris*). Turion leaves differ morphologically from normal foliage leaves such as those subtending the structure. Turions resist unfavorable environmental conditions and are efficient propagules for aquatic plants. (c) Severed or injured vegetative tissue is capable of generating "gemmaiparous" plantlets in several aquatic species, such as lake cress (*Neobeckia aquatica*). Detached leaves (shown here) or nearly any part of a lake cress plant (as small as 0.5 mm) can produce a gemmiparous plant. However, populations of this species have declined significantly because it is sexually sterile and the vegetative fragments function poorly in long-distance dispersal. Bars = 1 cm.

terparts in the terrestrial flora. Turions are dormant vegetative buds enclosed by specialized leaves that differ substantially in structure from normal foliage leaves. The often well-insulated turions are sometimes referred to as "winter buds," although in such species as *Potamogeton crispus* (Potamogetonaceae) they enable plants to overcome the stressful summer rather than winter season (Vierrsen 1993). The winter buds of terrestrial woody plants also fit this basic definition because their bud scales are modified leaves. However, buds of trees and shrubs remain viable only when attached to the parent plant and are incapable of dispersal and establishment. Detached turions of water plants are free-living propagules. In the extreme case of "asexual annuals" (Hutchinson 1975), turion production is accompanied by the decay of the remainder of the plant during periods of stress.

Other vegetative structures of dispersal in aquatic plants include "winter buds," which are enclosed by leaves not significantly modified from foliage leaves, and shoot fragments. Fragments play an important role in the vegetative reproduction of aquatic plants, with each individual node often capable of regeneration (Grier 1920). Many of the important aquatic weeds are dispersed in this fashion.

Yet another kind of vegetative propagule, gemmiparous (pseudoviviparous) plantlets (Figure 2c), are produced from leaves of some aquatic plants, including species of *Cardamine* and *Neobeckia* (Brassicaceae; Sculthorpe 1967), *Hygrophila* (Acanthaceae; Mühlberg 1980) and the so-called viviparous species of *Nymphaea* (Nymphaeaceae; Masters 1974). True vivipary (seedling growth while the fruit remains attached to the parent plant) occurs in the marine species *Amphibolis antarctica* (Cymodoceaceae). The small seedlings of *Amphibolis* (which are produced by sexual reproduction) eventually detach from the parent plant and are dispersed. Anchorage and establishment are assisted by a comblike structure that develops from the apex of the fruit and remains firmly attached to the seedling (Aston 1973). Vivipary in

Amphibolis suggests a compromise between sexual and asexual reproduction. Although viviparous seedlings possess the genetic advantages of a sexual derivation, the prerooted leafy stems can establish in much the same fashion as vegetative fragments.

Vegetative propagules of aquatic plants are dispersed by a variety of abiotic vectors (water, wind) and biotic agents (amphibians, birds, mammals, reptiles; Hutchinson 1975, Landolt 1986, Sculthorpe 1967). The minute size of plants in the duckweed family (Lemnaceae) facilitates the dispersal of whole individuals. In this family of the world's smallest angiosperms, individuals can be dispersed over several kilometers as a result of cyclones, and the smallest duckweeds (*Wolffia*) have even been found in hailstones (Landolt 1986). It is impressive that some species among these diminutive plants are also capable of producing yet smaller, vegetative turions (Landolt 1986). Ultimate versatility in vegetative dispersal structures is exemplified by the lake cress (*Neobeckia aquatica*), in which even minute root, stem, or leaf fragments (less than 0.5 mm) are capable of regenerating entire new individuals vegetatively.

Vegetative propagules have been instrumental in the dispersal of water plants by people. The adventitious rooting stems of watercress (*Nasturtium officinale*, Brassicaceae) were widely introduced throughout temperate regions, where they are used in salads (Sculthorpe 1967). Various countries import nonindigenous aquatic species and propagate them vegetatively for sale as ornamental aquarium and water garden plants. All species in the inventory of a recent North American water garden catalogue (William Tricker, Inc., in Independence, Ohio) were shipped either as whole plants or fragments. Most hardy water lilies are infertile hybrids and are propagated vegetatively (Swindells 1983). Although hybrid water lilies do not ordinarily become problems, shipments occasionally contain stems of nefarious weedy species such as *Hydrilla verticillata* (Hydrocharitaceae) draped around their rootstocks. The intentional or accidental release of cultivated, nonindigenous speci-

mens into natural habitats can lead to serious weed problems. The original presence of the notorious water hyacinth (*E. crassipes*) in the United States may have resulted from the careless disposal of souvenir plants (Sculthorpe 1967). The morphology of many aquatic plants contributes to their human-induced dispersal. For example, once introduced into a lake, the long stems of plants like *Elodea* (Hydrocharitaceae) and *Myriophyllum* easily become entangled on boat motors and trailers and are eventually transported to different sites.

The taxonomically widespread evolution of vagile vegetative propagules in aquatic plants is due to several factors. Particularly in temperate regions, where most natural lakes occur, aquatic habitats are not only short lived, but also subject to recurrent, catastrophic destruction due to glaciation. These events have undoubtedly selected for vagility in aquatic plants. Vagility of aquatic plants is not, however, exclusively a feature of vegetative propagules. Many species, such as marine angiosperms, rely on sexually derived seeds for their remote dispersal, and even the most clonal of aquatic angiosperms usually retain the ability to reproduce sexually. Indeed, only a few aquatic species, such as bladderwort (*Utricularia australis*, Lentibulariaceae) and lake cress (*Neobeckia*), are not known to produce viable seed (Les 1994, Taylor 1989). The rarity of lake cress underscores the importance of sexual reproduction to facilitate long-distance dispersal. This species has declined precariously throughout its historical range, despite a tremendous capacity for vegetative regeneration and local dispersal (Les 1994).

It is difficult to identify specific evolutionary factors that account for the widespread occurrence of asexual reproduction in water plants. Vegetative reproduction correlates highly with both polyploidy and hybridization in angiosperms. The importance of vegetative reproduction in stabilizing hybrid and polyploid reproduction (in which a diminished capacity for sexual reproduction is experienced) is well understood (Grant 1981, Les and

Philbrick 1993, Stebbins 1950). However, as Stebbins (1950) observed, it is unlikely that vegetative reproduction arose because of factors such as hybridization and polyploidy. Instead, it probably functions to maintain these conditions. Other factors have undoubtedly contributed to the prominence of vegetative reproduction in aquatic plants, and several hypotheses address this issue from contrasting perspectives.

Survival in aquatic habitats. Vegetative reproduction functions efficiently in aquatic environments, and water plants provide many examples of features associated with habitat-related survival. Reduction of mechanical tissue in vegetative organs of submersed aquatic plants is common and renders them fragile and susceptible to fragmentation by the action of waves, wind, currents, and interactions with biotic elements (Sculthorpe 1967). Although stem breakage and ensuing damage to water-conducting tissue (xylem) would have disastrous consequences for a terrestrial plant, harmful effects of fragmentation are mitigated by the absence or reduction of xylem in most submersed aquatic plants. Terrestrial plants rely on internal mechanical tissue to maintain an erect posture and to reduce breakage, whereas water lends external support to delicate aquatic plant shoots and helps to retain the viability of detached or fragmented tissues.

Fragmentation can also be observed in terrestrial species, such as the litter of tree branches that typically follows a windstorm or heavy rain. However, a major difference is that whereas aquatic plant fragments immediately find themselves in a habitat suitable for establishment (or are dispersed to other suitable sites), fragments of terrestrial plants usually require planting in the soil to survive (Hutchinson 1975). The protective aquatic environment allows the production of relatively fragile structures that excel in clonal reproduction (Grace 1993). At the same time, these structures are potentially more successful at colonization and subsequent population growth than sexually derived propagules because

they often root in the water before reaching suitable establishment sites (Barrett et al. 1993, Silander 1985). Furthermore, the proportion of aquatic habitats suitable for growth of vegetative propagules is much greater than that for seed germination (Sculthorpe 1967).

In many aquatic plants, particularly marine angiosperms, strongly rhizomatous growth forms (Figure 2a) help to resist the damaging forces of waves and tidal currents (Hartog 1970). An elaborate network of adventitious roots or rhizomes is required to withstand the loose and shifting substrates that characterize many aquatic habitats (Sculthorpe 1967). Rhizomatous growth is also advantageous to aquatic species by facilitating survival in habitats subject to periodic drought (Hutchinson 1975). Grace (1993) and Silander (1985) summarized additional advantages of clonal reproduction, including rapid numerical increase, unlimited production of favorable gene combinations, high vagility where spatial variation in favorable sites exists, efficient resource acquisition where resource limitation exists, and effective storage structures where large neighbors or a vernal environment predominates. The potential benefits of rhizomatous, or otherwise clonal, growth account at least partially for the high frequency of vegetative reproduction observed in both aquatic monocots and dicots.

Failure of sexual reproduction. Despite the intricate pollination mechanisms of some water plants (Cook 1988, Sculthorpe 1967), most aquatic plants retain the floral systems of their terrestrial ancestors, which were not originally adapted to function in water. Some species have acquired floral modifications that allow pollination to function efficiently in wet habitats, a phenomenon known as hydrophily. However, for species whose sexual organs are poorly adapted to aquatic habitats, clonal reproduction is an efficient alternative. Because asexual reproduction is a means of overcoming reliance on pollinators (Abrahamson 1980), it may facilitate adaptation to deep-water habitats where terrestrial pollinators do not

venture or under conditions in which the production of aerial flowers is difficult.

Sexual reproduction may fail in aquatic plants for several additional reasons (Barrett et al. 1993). Many aquatic species are distributed widely (Sculthorpe 1967), and individual plants may be incapable of adjusting their flowering responses to the myriad photoperiods, temperatures, and other environmental conditions that occur throughout a broad geographic range. Members of the vegetatively prolific duckweed family (Lemnaceae), for example, are widespread geographically, and flowering in these plants is influenced by many environmental factors (Landolt 1986). Almost all duckweed species retain the ability to flower, yet most are collected in flower less than 6% of the time and natural populations are much more likely to reproduce asexually than sexually (Landolt 1986).

Reduced flowering of aquatic plants in deep-water habitats is common (Hutchinson 1975). An obvious limitation on aerial flowering is that either stems or flower stalks must project from the surface. The deeper the plant, the more resources are necessary to produce a reproductive structure that reaches the water surface. Elongated reproductive structures are more likely to become physically damaged. This may explain why species such as *Butomus umbellatus* (Butomaceae) and *Gratiola aurea* (Scrophulariaceae) flower freely in their emergent forms but seldomly in their submersed forms (Hutchinson 1975, Sculthorpe 1967). Various depth-related physical factors, such as increased hydrostatic pressure, reduce the incidence of flowering in some aquatic species (Hutchinson 1975).

Although seed production is proportional to vegetative biomass in annual aquatic species (Vierssen 1993), it is likely that adaptation to vegetative reproduction in perennials has involved various energetic tradeoffs between vegetative and sexual reproduction due to resource limitations (Cook 1985, Grant 1981, Sculthorpe 1967). Such tradeoffs may result in a reduced level of flowering. For example, in *Potamogeton pectinatus*, tuber size and seed pro-

duction are inversely related (Yeo 1965). Several turion-forming species of *Utricularia* produce few flowers (Rossbach 1939). Some species of *Utricularia* are "vegetative apomicts," in which viable seed production has not been documented (Taylor 1989). Sexual reproduction in other species is displaced by vegetative reproduction. Vegetative turions develop in place of flowers in *Baldellia ranunculoides*, *Caldesia parnassifolia*, and in species of *Echinodorus* (Alismataceae; Hutchinson 1975, Sculthorpe 1967).

Sexual reproduction in clonal aquatic plants conceivably could also decline due to the accumulation of somatic mutations that influence sexual function. Nevertheless, the actual causes of limited sexual reproduction need to be studied more rigorously to determine how ecological, genetic, and other factors interact (Barrett et al. 1993).

Although sexual reproduction may often fail in aquatic habitats, many aquatic plants appear to be capable of persisting entirely by vegetative means. In the predominantly unisexually flowered family Hydrocharitaceae, several dioecious (male and female flowers on separate plants) species have become weedy even though only one sex had been introduced (Cook 1993, Hutchinson 1975, Sculthorpe 1967). Specific cases include *Elodea canadensis* (entirely female in Europe), *Egeria densa* (strictly male outside its native range), *Lagarosiphon major* (entirely female beyond its native range), and *H. verticillata* (female in its introduced ranges in southeastern United States and California). However, these examples offer evidence of only short-term survival. Once a prolific pest in Europe, *E. canadensis* has ultimately shown significant decline (Cook 1993). The cause is unclear, although ecological factors, including nutrient deficiencies, have been suggested. Whatever the reason for its decline, the case of *E. canadensis* indicates that exclusive vegetative reproduction in water plants may be insufficient to facilitate long-term adaptation to varying environmental conditions, particularly under dynamic selective regimes. There is evidence that limited sexual reproduction in adventive

clonal aquatic weeds limits their adaptive ability in nonindigenous ranges (Barrett et al. 1993).

Genetic uniformity. Asexual reproduction has been described as "any means of propagation that does not involve genetic recombination" (Abrahamson 1980). Therefore, widespread asexual reproduction in aquatic plants may have evolved as a means of maintaining genetic uniformity within populations (Les 1988a). In contrast to genetically diverse, sexually derived offspring, asexual reproduction can replicate optimally fit genotypes and maintain coadapted multigenic polymorphisms (Les 1988a, Silander 1985). In stable environments, the ability to clone superior genotypes by vegetative reproduction is arguably advantageous.

Many aquatic plants, particularly those with widespread distributions, possess broad ecological tolerances (Stuckey 1971). Wide ecological amplitude seems necessary because any changes in the water potentially influence all plants in contact with it. Consequently, aquatic habitats are less likely to provide "microsites" in which narrowly adapted genotypes may persist. Adaptation to dynamic water conditions is evident in widespread aquatic species such as *Lemna aequinoctialis* and *Lemna turionifera* (Lemnaceae), which can tolerate an extreme range of pH from 3.2 to more than 9.0 (Landolt 1986). The adaptation of aquatic plants to pH extremes is not surprising, given that diurnal pH variation within aquatic habitats alone can exceed two pH units; pH change can be stimulated by photosynthesis of submerged plants (Wetzel 1975). Once a species has broadly adapted to environmental extremes, vegetative reproduction assures that all future offspring will possess the appropriate genotype for surviving whatever conditions may be encountered during dispersal to new habitats (Les 1988a).

However, the hypothesis of genetic uniformity is problematic. Although clonally derived offspring are usually assumed to be identical genetically to their parents, somatic mutations can evidently generate significant variability in asexually de-

rived offspring (Les and Philbrick 1993, Silander 1985). Levels of genetic variability in asexual populations may even surpass those in sexual populations (Silander 1985). Recent studies of the vegetatively prolific lake cress (*N. aquatica*) have revealed surprisingly high levels of interpopulational genetic variation in this sexually sterile triploid.¹ Additional studies of genetic variation in clonal aquatic plant species are necessary to determine the degree of genetic uniformity both within and among their populations. Although the efficiency of vegetative reproduction should typically result in populations that are fairly homogeneous genetically, factors such as the immigration of genetically distinct vegetative propagules can result in more complex variational patterns (Les 1991).

Empirical documentation of natural genetic variation in aquatic plant populations exists for relatively few species. However, the available information suggests that aquatic plant populations are not altogether uniform genetically. Isozyme studies indicate that submersed species are characterized by limited levels of genetic variation, yet patterns of genetic variation in emergent aquatic species are, as in terrestrial species, associated with breeding systems and life histories (Barrett et al. 1993). Some aquatic plant species such as *Howellia aquatica* (Campanulaceae; Lesica et al. 1988) and *A. antarctica* (Waycott et al. 1996) appear to be entirely uniform genetically, but other submersed aquatic species possess substantial levels of genetic variation (Barrett et al. 1993).

Evidently, the level of genetic variability in aquatic plant populations is influenced by many interacting factors. Each aquatic plant species represents a unique, complex system of interacting life-history traits relating to particular reproductive, dispersal, establishment, and survival requirements (Waycott and Les 1996). Two monoecious, water-pollinated species, *Zostera marina* (Zosteraceae; a monocot) and *Ceratophyllum demersum* (Ceratophyllaceae; a dicot), provide a good

¹D. H. Les and J. D. Gabel, 1996, work in progress.

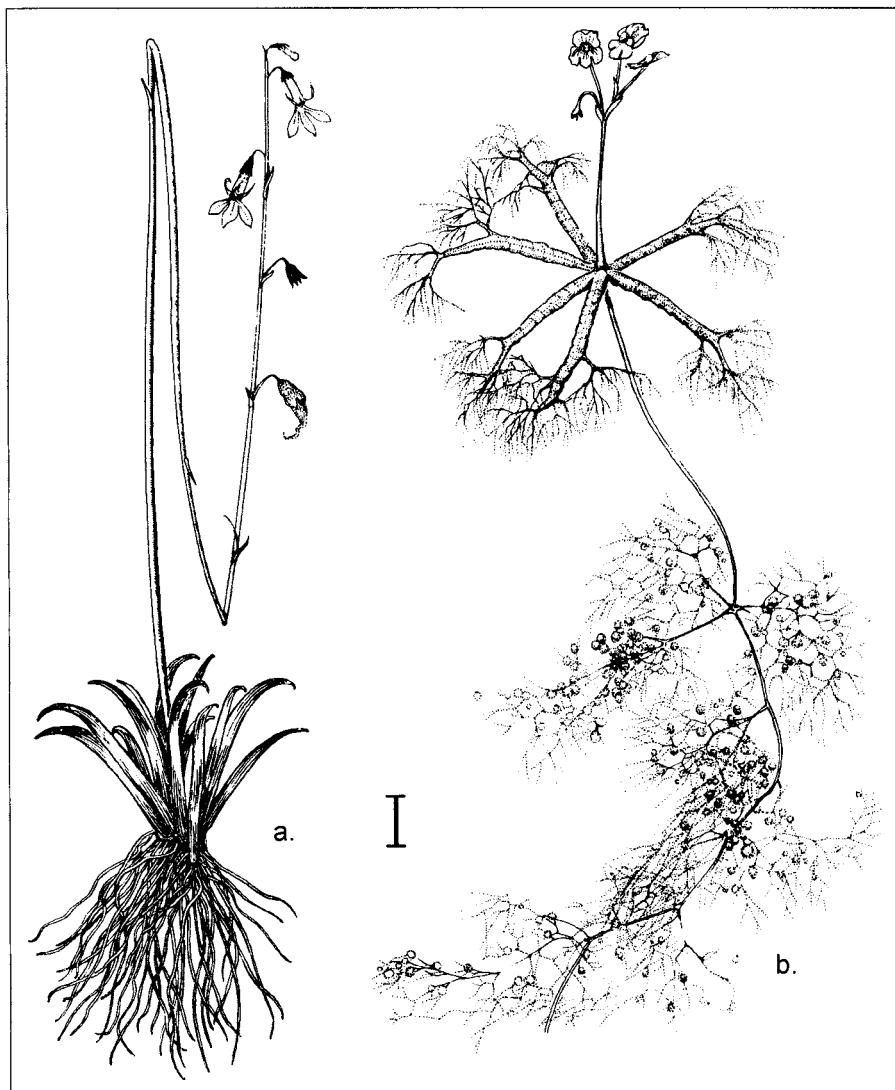


Figure 3. Submersed aquatic plants often possess highly modified vegetative organs but retain flowers with features similar to their terrestrial ancestors. Detrimental contact of flowers with water is prevented by a variety of contrivances. (a) This typical specimen of *Lobelia dortmanna* from Connecticut shows the exceptionally long floral stalks that extend from a completely submersed rosette of basal leaves. These flowers do not differ in any fundamental way from those of terrestrial *Lobelia* species. (b) Flowers of bladderwort (*Utricularia radiata*) resemble those of the closely related terrestrial snapdragons (Scrophulariaceae). A series of inflated "spongy floats" helps to prevent the contact of bladderwort flowers with the water, which may disrupt their function. The floats are modified portions of the highly dissected submerged stems, which contain bladders that trap small organisms for nutrition. Bar = 1 cm.

contrast. The incidence of sexual reproduction is much higher in *Z. marina* (Laushman 1993) than in *C. demersum* (Les 1991). Overall, the levels of genetic polymorphism are similar for both species, yet much more variation exists between populations in the latter than the former. Multiclonal populations are also far less common in *Ceratophyllum* (Laushman 1993, Les 1991). Reduced among-population genetic dif-

ferentiation and higher sexuality in *Z. marina* may reflect dispersal mechanism constraints. Although both species are perennial, *C. demersum* seldom produces seeds and disperses largely by vegetative propagules (Les 1991). In contrast, *Z. marina* spreads locally by rhizomatous growth (Laushman 1993) but has no principal means of long-distance dispersal other than by seeds (fruits). This finding may explain why

Z. marina commonly reproduces sexually and why different populations of this plant (which are founded by sexual propagules) show greater genetic cohesiveness than those of *C. demersum*. Certainly, higher levels of sexuality are expected in aquatic species that rely on seeds for dispersal. The pattern of genetic variation between and within populations will contrast widely across the wide range of tradeoffs between sexual and asexual reproduction that exists among aquatic plants.

Because vegetative reproduction is prevalent in most aquatic species, their life histories must be adapted to at least some degree of genetic uniformity. Still, it is difficult to determine whether vegetative reproduction has evolved principally to assure genetic uniformity or for some entirely different reason, with genetic uniformity as an inevitable consequence. Even if genetic uniformity were essential for aquatic plant survival, it could be achieved via either sexual or asexual means. A shift to inbreeding by self-pollination could conceivably result in the production of offspring that are as uniform genetically as those produced by vegetative reproduction. In any event, prolonged genetic uniformity seems unlikely for water plants, given that the genetically homogenizing effects of asexual reproduction can be offset by even sporadic sexual events that occur at some level in most aquatic plant species.

Sexual reproduction

Sexual reproduction by means of flowering, pollination, and seed production is a primary reproductive mode for terrestrial ancestors of aquatic plants. Although a shift from sexual to asexual (vegetative) reproduction is often associated with the evolution of aquatic plants, a complete absence of flowering and seed set characterizes only a few aquatic species (see above). The majority of aquatic angiosperms retain the ability to flower and set seed and do so, albeit sometimes rarely (Sculthorpe 1967). Sexual reproduction is obviously important to many aquatic groups, although its exact role remains to be elucidated. Yet it is

inappropriate to dismiss the importance of sexual reproduction in water plants. The elaborate contrivances that preserve floral function in aquatic habitats are unlikely to have evolved in water plants without selection to retain sexual reproduction. Moreover, water-mediated cross-pollination (hydrophily) is unique to aquatic plants and represents perhaps the most divergent shift in angiosperm pollination systems. Because the evolution of pollination systems has been central in the success of angiosperms, the novel origin of hydrophily in water plants further implicates the importance of sexual reproduction in their evolution.

The adaptation of angiosperm sexual reproductive systems to aquatic conditions must represent a difficult evolutionary transition. In many cases, angiosperms have acquired complex vegetative adaptations to aquatic habitats but have retained the aerial floral systems of terrestrial plants. Floral systems of aquatic plants are generally conservative and reflect their terrestrial heritage. Sculthorpe (1967, p. 245) wrote: "It is in their [sexual] reproductive phase that vascular hydrophytes betray their terrestrial ancestry with the greatest clarity." In bladderwort (*Utricularia* species), the submersed vegetative organs are so highly modified (Figure 3b) that typical morphological models of leaf and shoot structure are difficult to apply (Taylor 1989). In contrast, bladderwort flowers are aerial and possess both a structure and range of pollinators similar to that of terrestrial plants. Other aquatic plants in which highly modified vegetative structures occur in conjunction with aerial terrestrial flowers include *Megalodonta* (Asteraceae), *Limnophila* (Scrophulariaceae), and *Ranunculus* (Ranunculaceae).

The maintenance of pollination presents a particularly critical problem in wet environments. In most terrestrial and aquatic angiosperms, transfer of pollen to stigma is disrupted by contact with water. Because hydration is one of the first stages of pollen germination on the stigma (Richards 1986), contact with water sets in motion a series of biochemical events at the wrong time.

Pollen wetted by rain or water from another source becomes inviable due to premature germination or rupture (Corbet 1990). Evolutionarily, the pollination systems of aquatic angiosperms have remained functional in several ways. Some floral organs have adapted to avoid contact with water. Other flowers have acquired modifications that allow their terrestrial systems to function more efficiently in wet habitats. A few species have ultimately acquired adaptations for water pollination (hydrophily) in which pollen remains viable and is transported in direct contact with water.

Avoidance of water. Floral organs of aquatic plants avoid contact with water both directly and indirectly. In some aquatic species, dry reproductive organs are maintained by modified flowers that close and entrap an air bubble when pulled below the water surface. However, many aquatic plants overcome the detrimental effects of water by preventing the contact of aerial flowers with the surface. This is often facilitated by modified leaves, branches, and floral axes (Sculthorpe 1967). Groups of floating leaves reinforce aerial flowering axes in *Cabomba* and *Brasenia* (Cabombaceae), *Nymphoides* (Menyanthaceae), *Potamogeton* and *Callitriche* (Callitricaceae), some species of *Polygonum* (Polygonaceae), and *Ranunculus*. The floral axis of *Utricularia radiata* (Figure 3b) is supported by radiating "spongy floats" (Taylor 1989) composed of loosely packed, air-filled tissue. In *Hottonia inflata* (Primulaceae), the flower stalk itself (peduncle) is inflated (Sculthorpe 1967). Swollen upper stems of some *Myriophyllum* species provide a similar function (Crow and Hellquist 1983).

Flowers of aquatic plants often extend from the water surface on long stalks (Figure 3a). In *Lobelia dortmanna* (Lobeliaceae), aerial flowers project from the submersed rosettes on stalks up to 2 m long. *Nymphaea* and *Ranunculus* produce flowers that float at the end of long, resilient stalks that conform to surface motions and prevent the immersion of flowers by waves.

In some species of *Callitriche*,

which are self-fertile, pollen tubes avoid contact with water by growing internally through vegetative tissues as they pass from male (staminate) to female (pistillate) flowers of the plant (Philbrick and Anderson 1992).

Modifications to terrestrial pollination systems. The widespread maintenance of aerial flowers in aquatic angiosperms has led to the premise that the aquatic environment exerts little selective pressure on floral systems (Hutchinson 1975, Sculthorpe 1967). A closer examination of both biotic (mainly insect) and abiotic (wind, water) pollination systems reveals features that may be specific adaptations to the aquatic environment.

Flowers are disproportionately biased toward white color in aquatic plants (Sculthorpe 1967). We calculate that white flowers occur in approximately 43% of all aquatic genera (40% of dicots, 48% of monocots; based on data in Cook 1990). The high proportion of white flowers in water plants may enhance fitness by making flowers more conspicuous to pollinators. In the visible spectrum, dark flowers lack the contrast rendered by white petals against the dark background of water or floating vegetation. Because white petals are typically ultraviolet (UV) absorptive and water is UV reflective, white petals may also enhance contrast in the UV spectrum.

However, an alternative explanation for the frequency of white flowers in aquatic plants is that floral pigments in both the visible and UV spectra are under no selection in water plants. Angiosperms typically possess yellow flavonoid compounds that also serve as biochemical precursors to common floral pigments known as anthocyanins. Flavonoids are frequently lost in submersed tissues of aquatic plants (Les and Sheridan 1990). The white petals may simply reflect a background hue that results from the loss or lack of other floral pigments. In either case, white flower color would be highly convergent among water plants but unadaptive. Ecological and phylogenetic studies of aquatic genera such as *Ranunculus* and *Utricularia*, in which flower color varies among

species, could provide more meaningful insight into the significance of flower color in the aquatic environment. White can also be nonpigment related, as in the reflection of light from the intercellular spaces of petals (Faegri and Van der Pijl 1979).

The conservative nature of floral form in aquatic species predicts that water plants would share a similar suite of pollinators with terrestrial plants, yet there is little empirical data to support this claim. Some aquatic organisms, such as fish, have no apparent role in aquatic plant pollination, but recent studies indicate that the pollinator pool of water plants may include aquatic insects. Aquatic insects are diverse biologically, and many have life histories tied directly to aquatic plants. The association between aquatic insects and plants (flowers) is not typically related to floral rewards as it is in terrestrial plants. Most pollinators of terrestrial plants visit the flowers for collection of pollen and/or nectar. By contrast, aquatic insects use flowers for mating, shelter, protection from predators, and possible lairs for capturing prey. Aquatic insects make up varying proportions of the pollinator pool for several aquatic plant species. Two of the four primary pollinators of *Nuphar* (Nymphaeaceae) species are aquatic beetles (Coleoptera) and flies (Diptera; Schneider and Moore 1977). In *Nymphoides*, four of the six pollinators are aquatic insects (Diptera; Van Der Welde and Van Der Heijden 1981). In *Cabomba caroliniana*, four of the five pollinators are aquatic flies or bees (Hymenoptera; Schneider and Jeter 1982). Aquatic insects such as these may play an important part in the pollination of water plants and thus exert a unique suite of selective pressures on their floral evolution.

It was presumably because of selection in habitats disruptive to biotic systems that abiotic pollination systems evolved in angiosperms (Whitehead 1969). If the aquatic environment is inherently disruptive to biotic pollination, abiotic pollination should predominate in aquatic plants. Cook (1988), however, showed that the incidence of wind pollination in aquatic genera is only 31%, reflecting their ancestry from

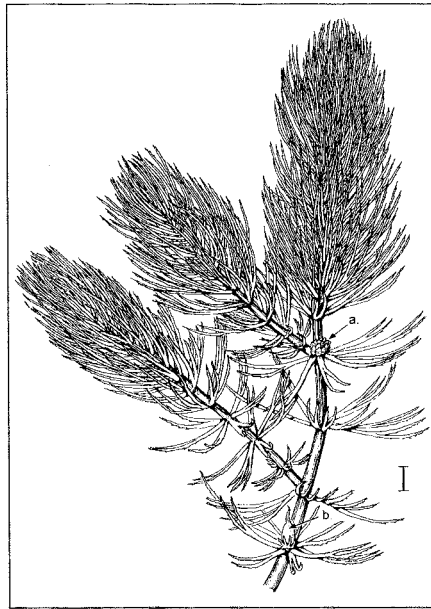


Figure 4. *Ceratophyllum* is a water-pollinated dicot with minute unisexual flowers. Pollen released underwater from dehiscing anthers (a) must pass through the water to a small opening in the side of the pistillate flower (b) to complete pollination. *Ceratophyllum* is an example of a species that carries out every aspect of its life cycle (except, perhaps, dispersal) in complete submergence. Bar = 1 cm.

terrestrial anemophilous (wind-pollinated) plants. *Limnobiium* (Hydrocharitaceae) and *Brasenia* are the only known aquatic genera that have seemingly shifted to an anemophilous pollination system subsequent to entering the aquatic environment (Cook 1988).

There is little evidence to suggest that anemophily in aquatic plants differs in any fundamental way from anemophily in terrestrial plants (Cook 1988). However, the trend for anemophilous terrestrial species of *Callitriche* to have pollen with a significantly thicker outer wall (exine) than related amphibious species (Philbrick and Osborn 1994) may represent the outcome of aquatic selective pressures. Little additional information is available on aspects of anemophily in aquatic angiosperms.

Hydrophily. Hydrophily (water pollination) represents a remarkable evolutionary departure from the pollination systems of terrestrial plants. In its most extreme form

(release and capture of wet, waterborne pollen), this abiotic pollination system entails structural and biochemical modifications of aerial pollination systems and the complete abandonment of aerial flowers. The perception that hydrophily is a general characteristic of aquatic plants is grossly misguided. Fewer than 130 aquatic plant species (less than 5% of aquatic species overall) in nine plant families (seven monocot, two dicot) are hydrophilous (Cox 1993, Les 1988a, Philbrick 1991).

The types of hydrophily have defied precise classification (Cox 1993). Moreover, the literature related to hydrophilous pollination is complicated by varying or vague use of terms (Philbrick and Anderson 1992; see Cox 1993, Les 1988a, and Philbrick 1988, 1991, for additional discussions and references). Two general classes of hydrophily occur in angiosperms—surface, two-dimensional and subsurface, three-dimensional—although distinctions between the types are not always clear. Subsurface, or underwater, pollination represents the most extreme modification of pollination systems to the aquatic environment. In this type of pollination, the flowers are submersed in the water, pollen is released underwater, and both pollen and stigma are functionally wet during pollination.

Hydrophilous species occupy freshwater, brackish (estuarine), and marine environments. Most genera that contain hydrophilous species are small taxonomically (less than ten species). The largest hydrophilous genus is *Najas*, with approximately 40 species (Cook 1990). Phylogenetic analyses of the angiosperm subclass Alismatidae (in which all hydrophilous monocots occur) reveals that hydrophily has evolved at least seven times.² Including *Callitriche* and *Ceratophyllum* (Figure 4), the only hydrophilous dicot genera, hydrophily has evolved as many as nine times in angiosperms. Although the evolution of hydrophily is complex, this system represents a striking convergence of aquatic plant pollination systems.

Hydrophilous pollination exhib-

²D. H. Les, M. A. Cleland, and M. Waycott, 1996, manuscript accepted for publication.

its notable examples of convergent evolution in angiosperm reproductive structures (Cox 1993, Philbrick 1991). Some modifications parallel those that have accompanied the evolution of wind pollination, such as loss or reduction of petals, high pollen production, low ovule number per ovary, small flower size, and unisexual flowers (Philbrick 1991). An impressive convergence involves changes in the exine and the manner of pollen dispersal. The exine of most hydrophilous species is extremely reduced or lacking. The exine in *Callitriche hermaphroditica*, *Ceratophyllum*, and the sea-grass *Thalassia hemprichii* (Hydrocharitaceae) is rudimentary (Philbrick and Osborn 1994). In species of *Najas* and the sea-grass *Amphibolis*, the exine is lacking altogether (see references in Philbrick and Osborn 1994).

Exine reduction in hydrophilous species represents one of few examples in angiosperms of a strong correlation between pollination type and pollen structure (Philbrick and Osborn 1994). The fundamental role of the exine—to protect the male gametophyte of terrestrial plant pollen (Richards 1986)—is evidently less critical when pollen is released in water. However, exine loss may not result exclusively from the relaxation of selection to prevent desiccation. Rather, there may be fitness advantages yet to be associated with the absence of a rigid exine. For terrestrial flowers, the exine also functions as a reservoir of substances involved in genetic self-incompatibility. Because such substances may be labile or rapidly leached out in water, selection for exine retention in water-pollinated plants may be minimal (Les 1988a).

Kress (1986) suggested that the exine is an end-point of selection on pollen–stigma interactions rather than on factors that operate during pollen transfer. Relationships among pollen dispersal, pollen–stigma interactions, pollen adherence, pollen germination, and reduction in the exine of hydrophilous species remain to be adequately assessed before a specific explanation for exine reduction in water-pollinated plants can be confidently accepted.

Pollen size, shape, and dispersal mechanisms illustrate convergent

trends among hydrophilous groups. Individual pollen grains in genera such as *Amphibolis* are often elongate and can reach remarkable lengths of 5 mm (references in Philbrick 1991) compared to the 20–40 μm diameter of average terrestrial plant pollen. Cox (1993) has interpreted the convergence of elongate pollen as evidence for the evolution of “search vehicles” that enhance pollen capture. This argument has been challenged by Ackerman (1995), who attributed the convergent shapes of hydrophile pollen to adaptive fluid dynamic design. Precocious pollen germination in water leads to a pollen:pollen–tube functional unit and may also increase pollination efficiency (Cox 1993, Les 1988a). Guo and Cook (1990) proposed that the stigmatic exudate of the hydrophilous *Zannichellia palustris* (Zannichelliaceae) stimulates pollen germination before actual contact between pollen and stigma.

Evolution of hydrophily. In angiosperms, pollinator shifts are often explained as responses to changing pollinator effectiveness. It is easy to envision selective pressures driving this transition in aquatic plants, particularly in marine habitats, where strong tidal fluctuations would render most aerial pollination systems inoperable. Hydrophily requires the loss or modification of characters that are intimately tied to dry, aerial flowering and thus represents a shift that is fundamentally different from transitions to all other pollination systems. The mechanical and biochemical modifications necessary for the evolution of pollen and stigma “wettability” (underwater release and capture of pollen) would seemingly raise significant adaptive obstacles not encountered during shifts from one type of aerial pollination system to another. Mechanisms to ensure pollination during such a dramatic transition in floral structure would be critical (Philbrick 1988).

The abandonment by angiosperms of highly conserved aerial floral biology for hydrophily is poorly understood (Philbrick 1988). Several factors have hindered the formulation of hypotheses concerning the evolution of hydrophily from aerial pollination systems. Floral features

of hydrophilous plants are divergent from those of aerial flowering groups (Cox 1993, Philbrick 1991), making it difficult to distinguish analogous from homologous structures. Furthermore, the phylogenetic relationships of water-pollinated species have historically been difficult to resolve (Les and Haynes 1995, Philbrick 1991). Finally, transitional stages that may have linked ancestral aerial pollination systems and derived hydrophilous systems have not been identified. It is difficult to envision how possible intermediate stages may have functioned.

Most hydrophilous systems have evidently evolved from anemophilous precursors (Les 1988a, b, Sculthorpe 1967). Both anemophily and hydrophily require significant modifications of floral structures found in biotically pollinated plants. We predict that the evolution of one abiotic system (hydrophily) would occur more easily from another abiotic system (anemophily) than from biotically pollinated ancestors. The transition may have been facilitated by the many parallel floral features of anemophily and hydrophily that are likely to represent general adaptations to abiotic pollination. This hypothesis is consistent with a phylogenetic analysis of water-pollinated monocotyledons (Les and Haynes 1995), in which lineages basal to all hydrophilous clades in the families Cymodoceaceae, Posidoniaceae, Ruppiaceae, Zannichelliaceae, and Zosteraceae are anemophilous.

However, the condition ancestral to hydrophily is less certain in the family Hydrocharitaceae, in which only one genus (*Limnobium*) is strictly anemophilous (Cook 1988). The surface-pollinated genus *Elo-dea* is particularly problematic, given that floral features in the tribe *Anacharitae* (to which it belongs) retain many floral adaptations for entomophily (insect pollination). Furthermore, two genera in the tribe, *Egeria* and the basal genus *Apal-anthe*,³ are entomophilous. The Hydrocharitaceae contain unusual pollination systems that are apparently derived from entomophily but employ wind to propel detached male

³See footnote 2.

flowers on the water surface (Cook 1988). This condition defies categorization as either anemophily or hydrophily but is obviously derived from entomophilous ancestors. Because this unusual system is likely to represent the ancestral condition of most hydrophilous Hydrocharitaceae, it is inaccurate to state that hydrophily in this family has arisen directly from anemophily.

Evolutionary models for hydrophily.

The preceding examples indicate that convergent hydrophilous reproduction has apparently evolved successfully from both biotic and abiotic systems. Therefore, it is not surprising that at least three contrasting models for the evolution of hydrophily can be proposed. Hydrophily may have evolved by gradual selection on aerial floral systems, leading to the accumulation of hydrophilous characters (the so-called gradual model). The range of pollination systems in the Hydrocharitaceae (Cook 1990) circumstantially supports this model. As described above, hydrophily in the marine Hydrocharitaceae and the genus *Najas* (merged by some authors in the Hydrocharitaceae) is connected phylogenetically to aerial biotic pollination by intermediate surface-pollination systems such as those found in *Enhalus* and *Vallisneria*. The intermediate condition consists of flowers that retain entomophilous features such as showy petals but are pollinated by detached, floating male flowers that either directly contact stigmas of female flowers with their anthers or aerially discharge pollen to the stigmas of female flowers. The system of floating flower reproduction in the Hydrocharitaceae could predictably lead to repeated contact of pollen with water and may select for adaptations to resist or accommodate wettability. However, even in *Elodea*, in which pollen is moved along the water surface, both pollen and stigmas remain dry (Cook 1988). Evolution of hydrophilous systems in the marine Hydrocharitaceae and *Najas*, in which both pollen and stigmas are completely wet, would represent a subsequent stage of adaptation in such a gradual model.

It remains unclear what selective pressures of the aquatic environment

are actually exerted on aerial flowers, even when they are in close proximity to the water. The conservative nature of angiosperm floral systems would predictably maintain aerial floral biology by strong stabilizing selection. Initial changes in pollen and flower structure would presumably occur with little disruption to aerial pollination; otherwise, features adaptive for hydrophily could destabilize reproduction. Phylogenetic studies indicate that unisexuality (monoecy, dioecy) preceded the evolution of hydrophily in the Hydrocharitaceae.⁴ This observation would necessitate that hydrophilous features evolved convergently in both male and female flowers. Nevertheless, this appears to have been the case with the Hydrocharitaceae, which illustrate a convincing example for the evolution of hydrophily by means of the gradual model.

The selfing-intermediate model is an elaboration of the gradual model (Philbrick 1988). In this model, self-pollination occupies a key intermediate position that allows hydrophilous features to accumulate while maintaining seed production. The self-pollination system in submerged flowers of *Potamogeton pusillus* exemplifies how such an intermediate pollination system might operate (Philbrick 1988). In this species, flowers open regardless of whether they are aerial or submerged. An elongation of the floral axis causes the flowers (which lack petals) to open. In *P. pusillus*, self-pollination occurs when pollen from dehiscent anthers moves to the stigma across a bubble surface. The bubbles originate as gases emanating from the dehiscing anther.

It is conceivable that selection for genotypes tolerant to pollen and stigma inundation could occur at such an air-bubble interface. Similar systems have been reported in the monocots *Groenlandia* (Potamogetonaceae; Guo and Cook 1990) and *Ruppia* (Ruppiaceae; Richardson 1976, Verhoeven 1979). Analogous systems that involve self-pollination between unisexual flowers on a plant (geitonogamy) have been described in the dicot *Callitriche* (Philbrick

and Anderson 1992). *Callitriche* is the only genus of flowering plants that is known to have both aerial and hydrophilous pollination systems (Philbrick 1993).

The selfing-intermediate model represents, perhaps, the simplest pathway to hydrophily. Self-pollination in submersed flowers is common in aquatics. Submersion of an aerial flower does not immediately require the acquisition of a fully functional hydrophilous system because the initial floral submergence is not tied directly to selection for hydrophily. Rather, increased fitness from self-pollination, not hydrophily, facilitates the abandonment of the aerial flowering condition. The selfing-intermediate model explains how genotypes with features necessary for hydrophily to operate can be selected for and become fixed in a population. Reproductive isolation occurs by self-pollination in submerged flowers. Because the ecological and evolutionary processes involved in this model are not complex, it is possible that many water-pollinated species evolved in a similar sequence. Hydrophily in most monocotyledons (excluding Hydrocharitaceae), and perhaps in the dicot *Callitriche*, has conceivably evolved in such a fashion.

A "punctuated" model is yet another possibility. Hydrophily may have evolved in one large step, with most hydrophilous features arising simultaneously. The suite of changes necessary for hydrophily to evolve in this way makes this model the least tenable of the three (Philbrick 1988). However, the dicot genus *Ceratophyllum* provides a possible example of punctuated hydrophily. *Ceratophyllum* appears to have descended from an early angiosperm lineage and possesses many reproductive features (branched pollen tubes, exineless pollen, monoecy, lack of stigma) that occur in the gymnosperm ancestors of flowering plants (Les 1988b). These primitive characteristics are convergent with features that have been derived in other hydrophilous angiosperms, presumably as adaptations to water pollination. Although most angiosperms never acquired hydrophily, the Ceratophyllaceae may have exploited this preadapted suite of

⁴See footnote 2.

primitive reproductive features to quickly adapt to hydrophilous pollination.

The rare condition of hydrophily is, nonetheless, polyphyletic in aquatic angiosperms, with at least nine separate origins. Although selective forces driving the drastic transition from aerial to submersed pollination may be similar for most aquatic plants, hydrophily is likely to have evolved by different processes among the taxonomically diverse groups in which it occurs. Attempts to generalize hydrophily should take into account the convergent nature of this reproductive system and consider each individual case of water pollination as a unique evolutionary event linked to different adaptive consequences. This conclusion is evidenced by the contrasting patterns of genetic variability that characterize populations of different water-pollinated species (Waycott and Les 1996).

Sexual reproduction and genetic variability. In this article, we have emphasized that the complex interaction of life-history traits, more than simply whether a species is principally sexual or asexual, determines how populations of aquatic species are structured genetically. Certainly a wide range of genetic variational patterns exists among aquatic angiosperm species (Barrett et al. 1993).

The influence of annual versus perennial growth on genetic patterns is an important consideration because annuals tend to be highly autogamous (self-pollinating) in both terrestrial and aquatic angiosperms (Barrett et al. 1993). Genetic uniformity, which is customarily associated with inbreeding, has been observed in aquatic annuals such as *Najas marina* (Triest 1989). Yet, unlike most annuals, *N. marina* does not conform to the general model that evolution of annuals is tied to efficient reproduction brought about by self-pollination, an impossibility in this dioecious species.

Self-pollination is often interpreted as adaptive where ecological factors deter cross-pollination (Richards 1986). Self-pollination is widespread in angiosperms and also occurs in many aquatic plants (Hutchinson 1975, Philbrick and

Anderson 1987, Sculthorpe 1967). It is unclear whether the incidence of self-pollination in aquatic plants varies significantly from the level observed in terrestrial habitats categorized as disruptive to pollination. Sculthorpe (1967) considered cleistogamy (pollination within closed, often submersed flowers) as "an evasion of the problems of elevating flowers above the water [surface]." Cleistogamy is in fact common in aquatic plants including *Myriophyllum* (Aiken 1981), *Podostemum* (Philbrick 1984), *Potamogeton* (Philbrick and Anderson 1987), *Ruppia* (Richardson 1976), and *Utricularia* (Taylor 1989). Both cleistogamy and selfing predictably lead to genetic uniformity. In this context we revisit a question similar to that encountered in the discussion of vegetative reproduction: Have selfing reproductive systems evolved in aquatic plants because of selection for genetic uniformity, or has selection for cleistogamy and selfing inevitably resulted in genetic uniformity? As before, the answer is elusive.

The evolution of some hydrophilous species is reasonably explained by a selfing-intermediate model in which selection for selfing precedes the gain of water-pollinated reproduction. Species that evolve in this fashion are likely to be characterized by low levels of genetic variation as a consequence of the selfing-intermediate stage.

Some amphibious species of *Callitriche* illustrate a unique means of reproduction by which genetic uniformity is maintained that blurs the distinction between sexual and asexual reproduction (Philbrick and Anderson 1992). Facultatively annual species such as *Callitriche heterophylla* and *Callitriche verna* set seed in abundance, but fertilization occurs by a system analogous to self-pollination within closed flower buds. However, species of *Callitriche* have unisexual flowers and lack perianth; thus cleistogamy in the usual sense is not possible. Instead, as discussed above, an unusual system of internal geitonogamy (Philbrick and Anderson 1992) results in which pollen grains germinate within undehisced anthers and pollen tubes pass internally through

vegetative tissues to female (pistillate) flowers of the same plant. Although seeds are produced in abundance, there seems to be little opportunity for cross-pollination. In these species, the sexual apparatus is maintained but genetic uniformity seems assured.

These examples demonstrate that the presence of sexual reproduction does not necessarily guarantee that an aquatic angiosperm species will comprise genetically variable populations. It is equally difficult to predict the level of genetic variation within a sexual aquatic plant species simply from its sexual condition (hermaphroditic, monoecious, or dioecious). Although unisexual reproductive systems such as monoecy and dioecy may promote outcrossing, they by no means guarantee it (Les 1988a, Waycott and Les 1996, Waycott et al. 1996). Breeding systems of aquatic angiosperms can vary substantially, even among species that are closely related phylogenetically, and disparate patterns of genetic variation exist even among biologically similar groups such as submersed, water-pollinated species (Waycott and Les 1996).

Conclusions

The highly convergent life-history traits of aquatic angiosperms make it nearly impossible to generalize about their reproductive system evolution. The small number of aquatic flowering plants presents an illusory perspective of biological similarity that vanishes on closer scrutiny. Aquatic plants are, in fact, an extremely heterogeneous assemblage of species that survive in similar habitats but as a result of fundamentally different evolutionary pathways.

Changes in reproduction have accompanied the invasion of the aquatic environment by several unrelated terrestrial plant lineages. Yet, except in rare cases, aquatic plants have merely exploited the reproductive features of their terrestrial ancestors by simple modifications. Many selective forces have molded the adoption of vegetative reproduction in aquatic plants as a major mechanism of population growth and even dispersal. Each aspect of veg-

etative reproduction has advantages and disadvantages, making it impossible to generalize that any one factor has been more influential than another. A rhizome may be an efficient organ of anchorage, yet provide no effective means of dispersal. Turions may be effective dispersal propagules but lack extended dormancy necessary for passing environmentally difficult periods.

Although vegetative reproduction provides angiosperms with important adaptations to aquatic habitats, evolution of aquatic plants has not proceeded toward total abandonment of sexual reproduction. Floral systems continue to play a central role in the population biology of aquatics, although how this role differs from that in terrestrial plants remains a challenging field of study. Every aquatic species has followed a unique evolutionary path that represents a complex balance between sexual and asexual reproduction, levels of genetic variation in offspring, and vagility to maximize survival. Because of the highly diverse evolutionary histories of aquatic plants it is difficult to identify general evolutionary models that apply to more than a few representative examples.

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Virtual Mentors Needed

The National Research Council's *Career Planning Center for Beginning Scientists and Engineers* (<http://www2.nas.edu/cpc>) provides information and guidance to students who are trying to get a job, planning their careers, or making educational choices. The Center has been very successful—so successful that we are seeking many new “virtual mentors” for the Advice Center of our Career Planning Center. All correspondence is by e-mail, so it is not too onerous a burden, and the benefits are many.

Mentors form a personal relationship with undergraduate and graduate students and postdocs and have the opportunity to discuss many issues, including ethical and ideological questions, as well as practical skills, such as how to write a good resume. Few pleasures are greater than that of inspiring and guiding enthusiastic younger scientists and engineers as they prepare to launch their own careers.

Mentors are especially needed in the disciplinary areas of **Ecology and Environment**. Mentors are also needed who can provide **general career guidance** (especially women or couples in dual science and engineering careers) and who have **nonacademic experience**, but mentors in all scientific and engineering areas are welcome because new students are requesting mentors all the time. For more information or to sign up to be a mentor, access the mentor form directly at <http://www2.nas.edu/cpcadv/mentor.html> or send an e-mail to ewojtasz@nas.edu (subject line: Mentor Volunteer).