FOUNDATIONS OF WETLAND SCIENCE EDUCATIONAL MODULES

The Education Section of SWS has developed a program, *Foundations of Wetland Science*, which is designed to provide the general public, students, instructors, and professionals with freely accessible online educational modules about wetland science for general knowledge or as resources for the classroom and outreach activities. The first two modules were published in *Wetland Science & Practice* this past April, and are also freely available to all on the SWS website (https://www.sws.org/education-modules-wetland-science/). Three new modules follow this introduction, and will also be posted on the SWS website.

We hope that the array of modules will grow over the years, and we encourage people who would like to develop a module on a topic of interest to them to contact the SWS Education Section Chair about their idea.

MODULE 3: INTRODUCTION TO WETLAND PLANTS

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OVERVIEW

This module is meant to provide a coarse-scale overview of some of the more important aspects of wetland plant biology. Covered here is a bit about the biology and ecology of wetland plants, as well as an overview of wetland plant taxonomic diversity. The topic of invasive species in wetlands is included as an example of one of many applied topics where the biology of wetland plants and animals has important intersections with society. Although the examples used here come predominantly (but not exclusively) from freshwater wetlands, the processes discussed are also important in brackish and saline wetlands.

WETLAND PLANTS DEFINED

As mentioned in Module 1, wetlands are a type of ecosystem typically defined, at least in part, by the presence of shallow water, or temporarily flooded or saturated soils during some or all of the biologically active period(s) of the year. However, as is also covered in Module 1, there is more to the definition than simply the presence of shallow water, otherwise, every puddle that forms after a rain shower could be called a wetland.

The depth of water is important, but so is the time of year during which standing water occurs and the length of time water is present. These factors influence biological and biogeochemical (biological + geological + chemical) conditions within a wetland, leading, under certain circumstances, to conditions that favor the development of wetland soils (a.k.a. hydric soils) and the establishment and persistence of wetland-adapted plant species. All three factors (water, soil, and plants) are intertwined in their influence on wetland characteristics, and this module will introduce some of the ways plants respond to the water and hydric soils in wetland ecosystems.

Wetland plants have been defined as those plants that are capable of establishing persistent populations in habitats where water is present at a sufficient depth and for a sufficient duration to have a biologically significant effect on the vegetation of the area. That effect is typically revealed in the characteristics of the plants and other organisms that live in the area from year to year. In the case of wetland plants, there are characteristic features of these species that indicate they would be expected to survive under the conditions created by the combination of standing water and hydric soils found in wetland ecosystems.

One such key feature in wetland plants is the presence of visible air passageways throughout their stems, roots, and leaves (Figure 1). These passageways often are associated with spongy tissues referred to as aerenchyma and provide many services to the plants, some of which will be discussed in more detail in later modules. However, one perhaps intuitive benefit of having air spaces throughout the leaves and stems of a plant living in an area with standing water is that the leaves and stems of the plant will be capable of floating at or near the surface of the water. Another benefit is that it shunts oxygen-rich air to the roots to support plant respiration. This floatation function of aerenchyma in wetland plants is a key feature that has led to a commonly used system for categorizing these plants.

It is estimated that there are more than 8,000 species of wetland plants in the United States alone (Lichvar et al. 2014). In an effort to simplify this diversity of plants and relate species to their roles in the ecosystem, biologists have devised a few classification schemes based on plant traits. The simplest of these divides wetland plants among four groups referred to as growth forms. These growth forms are emergent plants, floating-leafed plants, submersed plants, and floating (or free-floating) plants (Sculthorpe 1967; Figure 2).

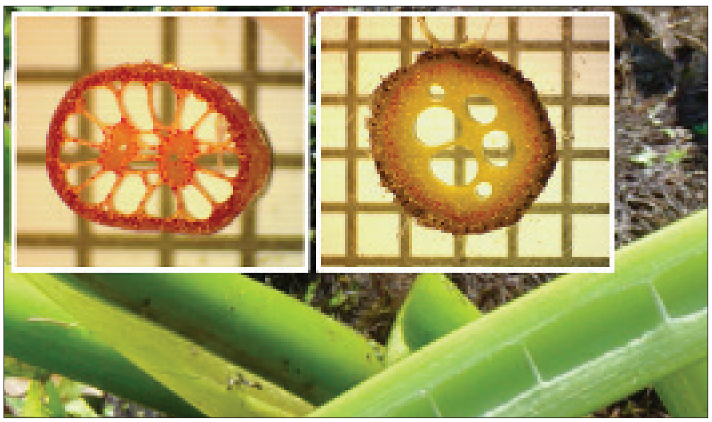

Figure 1. Examples of the air passageways (aerenchyma) that are common among wetland plants. The background shows a longitudinal section through the leaf stem (petiole) of Pontederia crassipes. *Inset photos in the upper-left are sectioned petioles of* Brasenia schreberi *(left) and* Nymphaea odorata *(right). Bottom-right insets are sections of a leaf (upper) and root (lower) of* Typha latifolia.

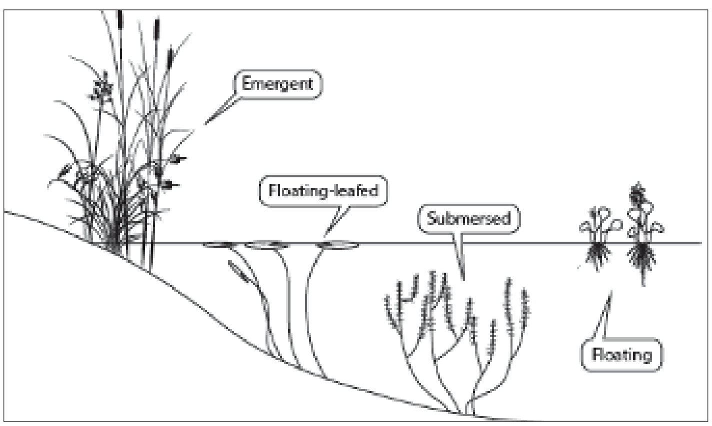

Figure 2. One commonly used scheme for categorizing wetland plants based on four growth form categories. Modified from Ervin (2023).

Emergent plants, which comprise the greatest diversity of species, are those that have their roots in the soil with their leaves and/or stems rising above the water surface. A few examples of emergent plants are shown in Figure 3A, but this group also includes species such as grasses, sedges, rushes, and cattails (Figure 3). Floating-leafed species typically have their roots and some form of belowground stem buried within the soil, with leaves floating atop the water surface at the end of long flexible stems called petioles. Examples of these are waterlilies. Submersed species, like the floating-leafed plants, usually have their roots buried in the soil, but their leaves and stems float suspended within the water. Most species (≥ 90%) of submersed species will have stem tips or flowers at or above the water surface, but most of the plant still will remain below the water. Examples of submersed species are *Hydrilla verticillata*, milfoils (*Myriophyllum* species), and many pondweed species (*Potamogeton* species). The final growth form, floating or free-floating species, are just that; these species float at or on the water surface with roots, if present, hanging below them in the water. *Pistia stratiotes*, *Pontederia crassipes*, the duckweeds, and some of the aquatic ferns are some widespread examples of free-floating plants. All these groups are found not only in fresh water but also in saline or brackish waters.

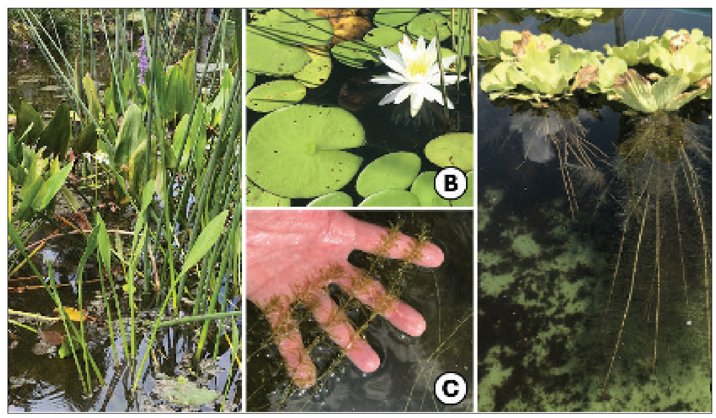

*Figure 3. A few examples from the four growth forms mentioned. A: Several species of emergent wetland plants, including arrowheads (*Sagittaria *species), rushes, and pickerelweed (*Pontederia cordata*); B: Floating-leafed plants (*Nymphaea odorata *and* Brasenia schreberi*); C: Submersed plant (*Hydrilla verticillata*); D: Floating, or free-floating plant (*Pistia stratiotes*).*

Three of these growth forms, floating-leafed, submersed, and floating species, benefit directly from the aerenchyma tissues mentioned above through the buoyancy provided by the internal air spaces. These species benefit by having their photosynthetic tissues held at, above, or near the water surface, placing them in the best position for capturing solar energy. This placement reduces the intensity of competition from other species for light. At the same time, the buoyancy provided by aerenchyma in the non-emergent growth forms reduces the need to produce supportive tissues that typically are found in the leaves and stems of emergent plants. This distinction between emergent plants and the other three groups is also reflected in the difference sometimes emphasized between wetland plants and the subset of those plants often referred to as aquatic plants. Aquatic plants typically are defined as those species who are supported by the water (via the buoyancy provided by aerenchyma) during all parts of their life cycles, and they make up a significant minority of all wetland plants, with only a few hundred species globally.

GROWTH FORMS AND WETLAND ZONATION

The great diversity of plant species present in wetlands makes organizing the floristics of these ecosystems somewhat complicated. There are thousands of species from among dozens of families, including everything from mosses and liverworts to cypress trees, mangroves, and sedges. The four-group scheme previously described (Figure 2) allows biologists to simplify this complexity to better study and understand the ecology of wetland plants.

This growth form classification system helps us think about the plants in light of some of their adaptations to the wetland environment while also reflecting their typical spatial organization within wetlands.

For example, emergent plant species, because their leaves and stems are physically supported above the water, can occupy a zone of wetland habitat along the water's edge. At the same time, because these species also produce aerenchyma tissue that helps to aerate their root systems and other belowground organs, they can live in saturated soils where non-wetland species would experience severe physiological stress. Thus, these species can escape competition from upland species while maintaining optimal exposure of leaves to sunlight above the water. As a result of their situation along the wetland edge, where water, sunlight, and soil nutrients are often in abundant supply, emergent plant species tend to be the most productive of the wetland plant growth forms.

Commonly, in the shallow water just beyond the fringe of emergent species habitat, floating-leafed species can be found to dominate the wetland flora. This is, to some degree, the result of their ability to tolerate deeper water than the emergent plants while also maintaining their photosynthetic tissues atop the water for maximal sun exposure. By having their roots in the soil at the bottom of the wetland, these species also have direct access to abundant soil nutrients.

Submersed plant species often have difficulty obtaining sufficient sunlight beneath the canopy of either emergent species or floating-leafed species. As a result, they are often relegated to deeper water, provided there is sufficient clarity to allow light to penetrate to the plant. Because most or all of their leaves are below water, their rates of photosynthesis will typically be lower than in emergent or floating-leafed species, despite having access to soil nutrients; seagrasses can be an exception to this rule. However, these species are very important in wetland and aquatic habitats because they provide dissolved oxygen and structural habitat for many aquatic invertebrates and foraging habitat for waterfowl, fish and other aquatic consumers.

Free-floating species are not confined to a particular zone within a wetland, by virtue of not being anchored within the wetland soil or sediments. However, these species do have an advantage in deeper waters by having direct access to sunlight, oxygen, and CO_2, and these species sometimes will be found to shade out the submersed species if they develop dense populations.

As a result of these behaviors of the four wetland plant growth forms, wetland vegetation often tends to be organized into zones from the water's edge out to the deeper portions of the wetland (Figure 2), although there often will be indistinct edges to the zones. This zonation plays into our understanding of wetland ecology, as well as our attempts to apply ecological understanding to solve problems such as water quality management with constructed wetland treatment systems. It has been found, for example, that different growth forms may complement one another in removing excess nutrients from contaminated waters (Vymazal 2007). Knowledge of the habitat requirements for the different growth forms, then, can facilitate could allow one to design a natural treatment system to efficiently improve water quality.

Some wetland scientists have developed much more complicated schemes for classifying wetland plants, in an effort to provide a more detailed summarization of the role vegetation plays in wetland function. Keddy, for example, used more than two dozen different plant traits to develop a functional classification of North American wetland plants (Keddy 2023). The traits examined included plant growth rates, stress tolerance, biomass allocation (above- vs. belowground plant parts), plant morphology, sexual vs. asexual reproductive strategies, and plant longevity (e.g., annuals vs. perennials). This and similar approaches based on species traits are useful because they simplify the complexity of ecological communities while still retaining key information about species based on how they interact with each other and with the physical environment.

MAJOR TAXONOMIC GROUPS OF WETLAND PLANTS

Wetland plants are found across a broad range of plant groups. Taxonomically, wetland plants exist among the bryophytes (mosses, hornworts, and liverworts), the ferns and "fern allies" (including clubmosses, horsetails, and ferns proper; Figure 4), the gymnosperms (fir, spruce, larch, cypress), and the angiosperms (the flowering plants; Ervin 2023). The first three of these groups (bryophytes, ferns, and gymnosperms) include only about 32,000 species in total globally, only some of which are adapted to wetlands. In contrast, the flowering plants number somewhere between 250,000 to 400,000 species globally, the uncertainty arising from incomplete exploration of many parts of the world and ongoing research into the genetic relatedness of known species and those that are regularly being discovered and described. Again, only a small percentage of these are adapted to wetlands, indicative of the powerful ecological selection imposed by the wetland environment. In the United States, for example, there are approximately 8,000 plant species recognized as wetland plants (US Army Corps of Engineers 2022), out of approximately 38,000 total species (~ 20%).

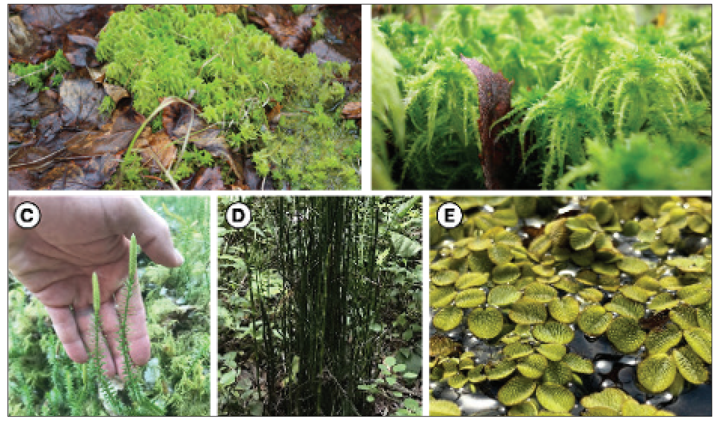

*Figure 4. Examples of sphagnum (*Sphagnum squarrosum*; A & B), clubmosses (C), horsetails (D), and aquatic ferns (E). Sphagnum photos courtesy of A: Tatiana Strus and B: Георгий Виноградов (Georgy Vinogradov), CC BY 4.0 <https://creativecommons.org/licenses/by/4.0>, via Wikimedia Commons.*

Among the mosses, *Sphagnum* species are probably best known, being important components of bog and fen communities, especially at the higher northern and southern latitudes. Ferns, horsetails, isoetids, and clubmosses are also commonly found in wetlands occupied by the mosses, but these species also are found in more temperate wetlands. Spruce (*Picea* species), fir (*Abies* species), and larch, or tamarack (*Larix* species), are often found in association with *Sphagnum* mosses in higher latitude peatland forests. In more temperate latitudes, river floodplain forests often serve as home to cypress (*Taxodium* species), many times in association with tupelos (*Nyssa* species, a genus of flowering plants).

Other trees within the angiosperms that often may be found in freshwater wetlands include the oaks (*Quercus* species), maples (*Acer* species), ash (*Fraxinus* species), and elms (*Ulmus* species). In saltwater habitats, another diverse group of trees is commonly encountered, that is the mangroves (Figure 5). Mangrove tree species come from more than fourteen somewhat distantly related families of plants, so they are defined by life form and habitat (i.e., trees that live in salt water) rather than by taxonomic relatedness. However, some of the more commonly recognized genera of mangrove tree species come from four families: red mangroves, *Rhizophora* species, from the Rhizophoraceae family, mangrove apple, *Sonneratia* species, from the Lythraceae, white mangrove, *Laguncularia*, from the Combretaceae, and the black mangroves, *Avicennia*, from the Acanthaceae.

Figure 5. Rhizophora mangle *(left) and* Avicennia germinans *(right) in southern Florida.*

Also in the angiosperms are a number of families with many species of herbaceous plants that are quite important in wetlands. Perhaps most well-known among those are the grass family (Poaceae; ~11,300 species globally), the sedge family (Cyperaceae; ~5,600 species globally), and the rushes (Juncaceae; ~400 species globally). Although not all grass, sedge, and rush species occur in wetlands, a large percentage do, and they often are ecologically important components of the flora in those wetlands (Figure 6). Other very important families among wetland angiosperms are the Alismataceae (~90 species), Hydrocharitaceae (~140 species), and Potamogetonaceae (~100 species), which include the majority of truly aquatic flowering plant species. That is, most of the plant species in these three families are highly adapted to life in the water, with many of them even relying on the water itself to carry out pollination. This is in contrast to the majority of other flowering plant families, whose members use the wind or insects for pollination.

*Figure 6. Lakeshore wetland in Rocky Mountain National Park, dominated by sedges (*Carex *species).*

One final group of plant families worth special mention are the families containing carnivorous plants (Figure 7). These species are often found in nutrient-poor highly acidic bog ecosystems, where they rely upon capture of insects and other small animals for part of their nutrition. Included among these are the Droseraceae (~200 species), which includes the sundews (*Drosera* species) and Venus flytraps (*Dionaea* species), the Sarraceniaceae (~30 species of pitcher-type plants; e.g., *Sarracenia*, *Darlingtonia*), and the Lentibulariaceae (~350 species), which includes the bladderworts (*Utricularia* species), among others.

Figure 7. Examples of some carnivorous wetland plants; Sarracenia alata *(left) and* Drosera rotundifolia *(right).*

INVASIVE SPECIES IN WETLANDS

Occasionally (although more commonly as the human population has expanded in size and interconnectedness), species may be introduced from wetlands in one part of the world to wetlands in another area, and some of those species might fit, ecologically speaking, differently into the community than does any one of the native species. This difference in ecological fit many times results in the newly introduced species having a competitive edge over many, or perhaps all, of the resident native species. There are many examples of such introduced species developing into highly invasive components of the ecosystem, overwhelming native species and causing important ecological and/or economic impacts to the invaded ecosystems.

A few noteworthy invasive plant species in wetlands are *Pontederia crassipes*, *Hydrilla verticillata*, *Myriophyllum* species, *Alternanthera philoxeroides*, *Phragmites australis*, *Phalaris arundinacea*, multiple species of salt marsh grasses (*Spartina* species in areas where they are not native), and floating aquatic ferns in the genus *Salvinia* (Table 1; Figure 8). These species have diverse histories, in terms of how they came to be introduced to other parts of the world, how they have impacted native communities, and how humans have responded in attempts to manage the invasion.

Figure 8. A few examples of noteworthy invasive aquatic and wetland plants. Clockwise, from top-left are: Pontederia crassipes, Myriophyllum spicatum, Alternanthera philoxeroides, Salvinia molesta, *and* Phragmites australis.

Although the sources of every introduction are not known, some of these species have been introduced in the horticulture trade because of their attractive flowers (e.g., *Pontederia crassipes* and *Lythrum salicaria*). In the case of *Lythrum salicaria*, those large showy flowers have co-opted native pollinators, who preferentially visit flowers of loosestrife, rather than the smaller flowers of native plants (Brown et al. 2002). Other wetland invaders have been introduced in association with the aquatic plant trade. Submersed species like the milfoils are especially susceptible to be introduced in this way because, as mentioned above, they provide excellent habitat for fish and other aquatic animals and help to oxygenate waterbodies. These services make submersed aquatic plants valuable components of home aquaria, but this also results in the occasional dumping of non-native species into local waters or in accidental escapes of non-native species into the wild from aquatic plant nurseries.

Common Name	Scientific Name	Origin	Region Invaded
Water hyacinth	*Pontederia crassipes*	Amazon basin in South America	Introduced into 146 countries worldwide; present on every continent but Antarctica
Hydrilla	*Hydrilla verticillata*	India and southeast Asia	Introduced into 40 countries; present on every continent but Antarctica
Eurasian watermilfoil	*Myriophyllum spicatum*	Europe, Asia, and northern Africa	Introduced into 19 countries; present on every continent but Antarctica; limited distribution in South America
Alligatorweed	*Alternanthera philoxeroides*	Paraná region of South America	Introduced into 27 countries; present on every continent but Antarctica
Giant salvinia	*Salvinia molesta*	Southeastern Brazil	Introduced into 61 countries; present on every continent but Antarctica
Common salvinia	*Salvinia minima*	Central and South America, from southern Mexico into Brazil and Argentina	Introduced into 4 countries; widespread in the western hemisphere but with very limited distribution in Europe, Asia, and Africa
Common reed	*Phragmites australis*	Native genotypes are known from many parts of this species' range	Recorded as introduced into 20 countries, but widespread occurrence of native genotypes complicates this species' biogeography
Saltmarsh cordgrass	*Spartina alterniflora*	Atlantic coast of North America	Introduced into at least 10 countries; known to hybridize with native Spartina species

Table 1. Origins and regions invaded by some common species of invasive aquatic and wetland plants. Origin as reported by USGS NAS database (2024); Region invaded based on data in GBIF (2024).

Free-floating species such as *Pontederia crassipes* and *Salvinia molesta* can have numerous negative impacts on aquatic and wetland habitats. For example, these species can shade the underlying water, resulting in decreased oxygenation of the water by submersed plants and algae, affecting populations of fish and other aquatic animals. They also can impede navigation of waterbodies causing economic impacts from reduced use of the water for transport and costs associated with managing the invasive populations.

In addition to the above well-known ecological or economic impacts, invasive plants can sometimes have less obvious impacts, such as hybridization with native species or introduction of non-native genotypes into different parts of a species' global range. Invasion by salt marsh grasses in the genus *Spartina*, for example, have led to hybridization between native and non-native *Spartina* species, forming hybrids that eventually invaded local wetlands, outcompeting native species of *Spartina* and other native plants. In fact, until relatively recently, it was thought that *Spartina alterniflora* was native to both North and South America. Bortolus and colleagues (2015), however, have provided several pieces of evidence suggesting this species was introduced into South America, rather than originating there. In the case of *Phragmites australis*, there are genotypes that are considered native to the United States, but multiple genotypes have also been introduced into the US, sometimes complicating conservation efforts for this species and wetlands it occupies (Saltonstall 2002; Kettering and Mock 2012).

Management of invasive plant populations can involve physical or mechanical disruption of local ecosystems through efforts to harvest and remove plant material, application of herbicides to kills the invasive species, or introduction of herbivores meant to control the nuisance plant populations. This latter management approach, termed biological control (biocontrol for short), has made use of highly specialized herbivorous insects to target the introduced plant species or generalist herbivores, such as grass carp, for the wholesale removal of vegetation in invaded habitats. The use of specialist insects has been attempted for control of invasive aquatic plants (Figure 9), but long-term success of these efforts typically requires repeated releases of the insects. In the case of the generalist fish herbivores, there are many examples of these species escaping from managed waterbodies and invading other habitats, leading to negative impacts on native aquatic communities and impeding use of the waterbodies by people. Physical collection of plants must be conducted carefully, especially with free-floating species, as small segments of plants left behind often regenerate into complete plants.

*Figure 9. Specialist insects introduced into the United States as potential biological control agents for invasive plants. Left: alligatorweed thrips (*Amynothrips andersoni*) on* Alternanthera philoxeroides *(at tips of black arrows); Right: water hyacinth planthopper (*Megamelus scutellaris*) on* Pontederia crassipes.

There also are many examples of introduced animals affecting wetland vegetation. Many of these are mammalian herbivores. For example, the nutria (*Myocastor coypus*) was introduced into North America as part of the fur trade, and it has had substantial impacts on coastal wetlands of the Gulf of Mexico and Atlantic coast of the US. Beaver (*Castor* species) similarly have been introduced outside their native range, where they have impacted local wetlands, as have water buffalo (*Bubalus bubalis*) and wild hogs (*Sus scrofa*). The Everglades, a large complex of wetlands in southern Florida (US) have experienced substantial numbers of invasions, not just by plants, but also by animal herbivores, and predators. Well known invaders in the Everglades include green iguanas (*Iguana iguana*), pythons, snails, and cane toads (*Rhinella marina*), but many more are present. In fact, it is estimated that there are more than 130 species of invasive animals in the Everglades.

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