Mangrove Swamp Communities: An approach in Belize

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Abstract

Belize has the longest barrier reef of the northern hemisphere, extending 220 kilometers from Mexican border in the north to the Gulf of Honduras in the south. Behind this barrier lies an enormous lagoon system averaging 25 kilometers between the mainland and open ocean. Mangrove bordermost the coastline, extend upstream of the countless river mouth and fringe or cover most lagoon cays. Two Caicais have become our study site and experimental laboratory. The purpose of this chapter is document the biology, geology, ecological balance, economic importance, and aesthetic value of a prominent coastal ecosystem.

The inventory of species has yet to be compiled, but the most flashy are represented by species of which 10 to 25 percent, and in some microscopic-sized groups up to 60 percent, are undescribed.

Resumen

Belize posee la barriera arrecifal mas grande del hemisferio norte, extendiéndose 220 kilòmetros desde el borde mexicano al norte, hasta el Golfo de Honduras al sur. Detrás de esta barriera se sitúa un enorme sistema lagunar (promediando 25 km entre el continente y el mar abierto). Los manglares, que bordean la mayor parte de la línea de costa, se extienden no sólo por las innumerables islas del río y cubren la mayoría de los cayos lagunares. La biología de los arrecifes y la biología experimental se encuentra en las Caicais. El propósito de este capítulo es documentar la biología, geología, balance ecológico, importancia económica y valor estético de este notable ecosistema costero.

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The roots gave of clicking sounds, and the odor was disgusting. We felt that we were watching something horrible. No one knew the mangroves. That is how James Steinbeck and E.F. Ricketts depicted the mangroves in 1941 in the "Sea of Cortez." Many people will agree with them. So why have two dozen scientists from the Smithsonian Institution, primarily the National Museum of Natural History, and twice as many colleagues from American and European universities and museums devoted a decade of exploration to one square kilometer of "Black Mud... flies and insects in great numbers..."

Properties of Mangrove Swamps

Mangrove swamp communities dominate the world's tropical and subtropical coasts, paralleling the geographical distribution of coral reefs.

Mangroves on the Atlantic side of the American coasts occur between Bermuda and the mouth of the Rio de la Plata and throughout the West Indies. Like reefs, mangrove swamps are environments formed by organisms, but unlike most coral communities, they thrive in the intertidal zone and endure a wide range of salinities.

"Mangrove" refers to an assemblage of plants from at least five families with common ecological, morphological, and physiological characteristics that allow them to live in tidal swamps. Worldwide, at least 34 species in nine genera are considered to be true mangroves. P.B. Tomlinson's recent book "Flotation of Mangroves" defines this group of plants by five features: 1) they are ecologically restricted to tidal swamps; 2) the major element of the community frequently forms pure stands; 3) the plants are morphology-adapted to aerial roots and evapotranspiration (producing new plants instead of seeds); 4) they are physiologically adapted for salt exclusion or salt excretion; 5) they are taxonomically isolated from terrestrial relatives, at least at the generic level. "Mangrove swamp" or "mangal" refers to communities characterized by mangrove plants.

Mangrove trees are used for wicker-resistant timber, charcoal, tannins, dyes, and medicines. They resist coastal erosion during storms and have the reputation of promoting larval-building processes by trapping sediment and producing peat. The protective subtidal root system of red mangrove is cultured as serving as nursery ground for many commercially valuable species of fish, shrimp, lobsters, crabs, mussels, and oysters. An attractive fauna of birds, reptiles, and mammals is also at home in the mangrove thickets and tidal channels.

Human disturbances have made a heavy impact on many mangroves near populated areas as a result of dredging and filling, overcutting, insect control, and garbage and sewage dumping. The intertidal environment of mangroves is endangered by pollutants in water, air, as well as in the soil. Accidental oil spills appear to be particularly damaging. Oil and tar (for only smoother algae and invertebrates, but also disrupt the oxygen supply to the root system of the mangrove trees by coating the respiratory pores of the intertidal roots and air roots.)
Belize (formerly British Honduras), boasts the longest barrier reef of the northern Caribbean, extending 250 kilometers from the Mexican border in the north to the Gulf of Honduras in the south. Behind this barrier lies an enormous lagoon system averaging 25 kilometers between the mainland and open ocean. Mangroves border most of the coastlines, extend upstream of the countless river mouths, and fringe or cover most lagoon cays.

One of these is Twin Cays (Fig. 1)—an island divided into two by an S-shaped channel. Twin Cays has become our study site and experimental field laboratory. Although we usually spend the nights and conduct lab work on nearby Carrie Bow Cay—site of the National Museum’s coral reef field station for 20 years (founded in 1972)—most days and many nights are spent in the mangrove channels, lakes, ponds, mudflats, and even the trees. Many important climatic parameters are recorded by a self-contained weather station on Carrie Bow Cay. Selected ichthyographic measurements, such as tide, temperature, turbidity, salinity, are recorded at substations in the swamp. The bibliographies on mangroves show that during the last 200 years more than 6,000 papers have been published describing biological and geological details from

![Map of study area. Twin Cays, Belize. The National Museum of Natural History's coral reef field station is located on Carrie Cay, about four kilometers southeast.](image-url)
Figure 1. Map of study area, Twin Cays, Belize. The National Museum of Natural History's coral reef field station is located on Caribe Cay, about four kilometers southwest, (from Rützler and Macarmac, 1982, Smithsonian Contributions to the Marine Sciences 13).

A Mangrove Laboratory in Belize

Belize (formerly British Honduras), boasts the longest barrier reef of the northern hemisphere, extending 225 kilometers from the Mexican border in the north to the Gulf of Honduras in the south. Behind this barrier lies an enormous lagoon system averaging 25 kilometers between the mainland and ideal ocean. Mangroves border most of the coastline, extend upstream of the countless river mouths, and fringe or cover most lagoon cays.

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almost as many different species as the world. Our ongoing study aims to analyze as many components as possible of a single zebra-gra

Geological History of Twin Cays

A popular theory holds that mangroves are builders of land because they trap and hold fine sediments. Easily on our way we discovered that this is not necessarily true. We tried to rearm me from Curlew Cay, which had been pushed to a hurricane (it is now known as Curlew Bank), by planting an assumption of young red mangroves, but they were unsuccessful. So the question arose, it is not built by mangroves, how do they get started?

To learn more about the Holocene (recent time—back to 10,000 years before present) stratigraphy under the ancient island, Ian G. McIn-

tyre of the Smithsonian Museum of Paleontology, along with Robin L. Lighty and Alan Raymond of Texas A&M University, drove pipes 1 m into the sediments about 2 m above the Holocene level (mark the beginning of the Holocene), and retrieved sediment cores which date back several thousand years, the maximum sediment accumulation in this particular area. They also collected rock cores below this level. What they found below the mangroves was a swamp and, ultimately, assembled them to a mosaic reflecting structurally as well as function of this unique ecosystem.

Environments Below the Tides

The bottom of the mangrove (Fig. 2), from the intertidal to three meters, is grazed by fish and fallen plants. It is composed of what most people would call mud. To us it displays many variables, such as carbonates, mud, and sand, with varying amounts of mussels, organic detritus (products of plant and animal decay), peat, and silicious skeleton derived from dinoflagellate and sponges. Many fine-grained intertidal and subtidal sediments are produced by physical and biological erosion on the nearshore sediments and transported into the mangroves by tidal currents. Sand, on the other hand, is primarily produced within the community by deposition of decay of calcareous green algae (Halimeda).

The most abundant and ecologically important plant on this intertidal area is the burrowing grass (Thalasmia), it stabilizes the mu-
daby bottom, offers substrates for egg masses and many small invertebrates, and provides food and shelter to animal grazers ranging from micro- to macroinvertebrates. Burrowing is a seagrass ecologist from the University of Wesley-

nia, determined that burrowing grass in the Twin Cays mangrove is a dominant and provides three times faster than the seagrass in the nearby open lagoon, resulting in an almost 10 times less net yield production.

Red mangrove salt striata root line all channels, creeks, and ponds and, below tide level, support typically colored clusters of algae, sponges, tunicates (sea squirts), anemones, and many associated. They also provide hiding places for many small animals, such as crab, lobsters, sea urchins, and fishes.

Algae without the ability to root in mud bottoms abound in the tidal flats. Mark Utter, from the Smithsonian Institution of Botany, and research- ers Pierre Utter and Phillips Taylor found that, curiously, fistly algae seem to prefer roots that had penetrated the water surface but had yet reached the bottom of the channel or lagoon. Calci-
fying algae (such as the sand-producing Halimeda), on the other hand, are common on the submerged parts of seagrass roots and along the channel banks. Experiments demonstrated that the hanging roots offer protection from herbivorous fish, such as sea urchins and mantis shrimps, whereas Halimeda has its own skeletal protection.

Certain algae and many invertebrates cemented on the subtidal mangrove roots are protected from predators by toxic substances stored in their tissues and produced by their own metabo-

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their antibiotic and feeding-detergent properties and are used by many smaller organisms, such as amphipods, polychaete worms, shrimp, crabs, and mollusks as an effective physical and chemical shelter. Collaborating with our Smithsonian colleagues Kristian Fauchald, Gordon Hammersley (now at the Los Angeles County Museum), and Brian Kembel, we extracted up to 40 species and 400 epizoans of echinoderms larger than 2.5 millimeters from, as an example, a 1-liter fire sponge (Ianthina), a species that causes burning, itching, and even severe dermatitis in humans.

Sponges are among the most common, massive, and colorful invertebrates in the submerged mangrove. To settle and mete-morphose, their larvae need solid substrate with low exposure to sedimentation, although we observed growing sponges surviving for months buried in light mud after they had fallen from their places of original attachment. Only two kinds of firm substrates are available to such settlers, red mangrove still roots, and verthos or overhanging banks composed of a past and live mangrove roots and flushed by tidal currents.

In both locations, the competition for space is fierce, not only among sponges but also between sponges and other sessile organisms, such as sponges, hydroids, the (polyp) generation of many ascidians, corals, anemones, bryozoans (moss animals), and barnacles (sea squirts). With our colleagues Dale Caldar, Royal Ontario Museum, Ivan Donnelly, University of the West Indies, and Jan Kikoinsky, University of North Carolina, we are analyzing the sequence of settlement of species at different seasons, following their growth and subsequently the methods and hierarchies of composition.

We have found that within days new substrates (wood, plastic) are colonized by ubiquitous bacteria, fungi, and lower algae. The next to arrive are crystalline algal crusts, sponges, hydroids, deypoxoan polys (the polyp stage of
the upside-down jellyfish Cassiopeia, anemo-
nom, serpulid and sialid worms, bryozoans, and pelecypods. After 2 to 3 months, substrates are fully covered by a spectrum of organisms. The spectrum varies greatly and depends on the season in which the experiment was started, the habitat position of the substrate, and the environ-
mental endurance of the settlers.

Not all subtidal mangrove leaf is restricted to the bottom and roots. Fishes of all size and age classes hide or feed in the water column around the red mangrove roots and along the banks. Many of these depend on plankton, such as copepod and mysid crustaceans, for food. Mem-
bers of both groups form characteristic swarms during the day. Smithsonian's Frank Kerr teat-
ied up with Julie Amsler, Texas A & M Univer-
sity, Arv Boodhan, University of Adelaide, and Richard Modlin, University of Alabama, to study the systematics, ecology, and genetics of the swarms and found population densities much greater than expected. They obtained more than two thousand copepods per cubic meter of water in a small bay at night, and estimated 100 million individual copepods gathered during the day in a hand of swarms along a 1,000-meter stretch of channel bank.

The Intertidal Mangrove Swamp

Although the tidal range in the Caribbean is small, in shallow coastal areas it can strongly influence current flow and distribution of orga-
nisms. At Turn Caye, the mean tidal range is only 15 centimeters, yet a combination of astro-
nomic, geomorphologic, and meteorologic factors can cause a range of 20 more than a half meter.

Red mangrove (Rhizophora) young roots, black mangrove (Avicennia) pneumatophores (facial roots), peat banks, and mudflats are the typical substrates of the intertidal zone supporting dis-
crete communities. Bamboos (Chromeleon), wind-breaking thickets (Lumniera), eysters (Cassiopea), and "mangrove oysters" (Sagun-
mon, not a true oyster) are the best known indicators of intertidal hard substrates, while tidal flats (Boca) are typical for the mud flats.

Korin algal mats (Ceratophyllum, Hemipedia) are found exposed on protected banks during low tide. The mud abundant and characteristic inter-
tidal mangrove community, however, is called the botryochydom at the high tide. The principal compo-
nents of an association of wet algal (Botryochydom, with Catanella and Celsiochaeta).

The botryochydom (Fig. 3) has a remarkable water-building capacity, which allows the plants and their associated animals to survive exten-
ded dry periods. We measured water loss rates in two of the substrate species and found eviden-
ce of two different methods of water retention. Botryochydom is a delicate, tufted plant that holds water primarily by turgidity (between the bran-
ches). Catanella is more fleshy and less turgidly branched and holds water intracellularly (within the cell) in its tissue.

Loren Coen, Doughlin Island Marine Labora-
tory, examined the animal associates of the bot-
ryochydom, particularly in respect to grazing. He found graziers nothocheps (Protarchaeon) to be com-
centrated in the algal mats in ny's hard

during ascending tides, and that their grazing on Botryochydom can match or exceed the algal growth. The mangrove tree crab Anatus, and other crabs from low tide level were also found with large quantities of Botryochydom in their guts.

Desiccation and related problems of increas-
ing temperature and salinity in organisms sub-
exposed to exposure at low tide become partic-
ularly apparent during an extreme low tide in June, 1985. A 20-centimeter zone below mean low tide level became exposed during noon hours under a clear sky. Large communities of low intertidal (tang exposed) and subtidal (ne-
ver exposed) organisms, such as occupant of seagrass meadows (including the turf grass itself), and mangrove mud banks and soft roots, were killed during the long exposure to desiccation. Estimates indicate that more species of algae and invertebrates, and much more living matter (biomass), were destroyed during those days of June than during two hurricanes combi-
ined (Flitt, 1974; Grela, 1978).

Graziers that physiologist Jean Ferraris, National Institutes of Health, is experimentally examining a number of organisms (sponges, sipunculous worms, shrimps, crabs) that are ex-
posed to strong salinity-temperature stress in their natural environment. Results so far show a fine correlation between experimental tolerances in the animals and range of variability of stress factors in their natural habitat. In the case of sponges, regulatory mechanisms controlling water-ion exchanges are strongly expressed, but in absence of organs they must take place inside individual cells.

Unfortunately, the intertidal swamp is not only an exciting biological study zone but also a ga-
llery of pollutants. Even in this remote location, some imaginable piece of floating debris discar-
ded by man can be found. washed in by currents among the mangrove roots and deposited by the receding tides.
Mangrove Forest Above the Tide

Unlike the adjacent marine systems, the supratidal flora and fauna of the mangrove-covered islands appear less complex and diverse. From the water, an unbroken, monotonous barrier of red mangrove and related forms, and frequently tamarisks, constitutes the coastal explorer.

The specific composition of the supratidal plant community around Two Cays is relatively simple. Three halophytic tree species, known collectively as mangroves, dominate the natural vegetation on most of the islands: red mangrove (Rhizophora mangle), black mangrove (Avicennia germinans), and white mangrove (Laguncularia racemosa). On cays with slightly higher ground, additional woody and herbaceous halophytes are associated with the mangrove, such as buttonwood (Conocarpus), saltwort (Salsola), and sea purslane (Sesuvium).

In general, mangrove forests have well-defined horizontal zonation. On these mangrove islands, the seaweed and channel margins typically are fringed by dense, 4 to 10-m high stands of red mangrove. Behind this fringe, the forest is usually more open and shorter, with black and white mangroves intermixed. The zonation is easily recognized: dull gray-green spikes of black mangrove, and flattened, yellow-green crowns of white mangrove stand slightly above and behind the dark green dense of the fringing red mangrove.
The interior of some of the larger islands off Bimini, like Twin Cays, have several extensive, un見たged mudflats and shallow ponds. Nau- merous slumps throughout the mudflats are evi- dent that the tides that once grew these mollusks victim to some environmental stress. The red mangrove trees growing on the mudflats and in the ponds are severely stunted and widely spaced. Over the years, the natural beauty has been distorted and graded by their environment into fantastic forms, similar over 1.5 meters tall. A. Lugo and S. Shideler in their 1974 review of mangrove ecology, esti- mated the age of comparable dwarf trees in south Florida and the Florida Keys to be 40 years old. Our collaborator Irving A. Mendelsohn, Karen McCool, and Colin D. Wood broads (Florida Biogeography Institute, Louisiana State Uni- versity) suggest that abiotic factors, such as high soil sulfides levels in the soils, may be responsible for the die-back and reduced tree vigor.

The supertidal faunas on the cays is considered by most investigators to be introduced from the Belize mainland. Even on the largest mangro- ve islands, most of the "land" is intertidal; therefore, the only environments available to terrestrial animals are arboreal. This fauna is limited to birds, lizards, snakes, snails, and arthropods, such as land crabs, spiders, and insects. These animals probably reached the cays from the mainland by flying, rafting on or in pieces of wood or other floating debris.

Several land birds species have established breeding colonies on the cays, and they have felled the island vegetation. James F. Lynch (Smithsonian Envi- ronmental Research Center) reports that the mangrove yellow warbler is the most charac- teristic land bird throughout the cays, but the Yucatan vireo is also a well-established resident on most of the cays. Both of these species are insectivorous. The hummingbird, Amerisbico- rax, has been observed nesting in red mangrove on Twin Cays but not on smaller islands. Man- grove crabs, grackles, and white-crowned pigeons, common on the large mangrove islands, are also thought to be permanently resident. Several of the islands also provide nesting sites for ospreys. These birds frequently build their nests in the snags of black mangroves.

At Twin Cays, the diapper race with its loud, rather sudden clatter is more often heard than seen, although occasionally one can catch a glimpse of it walking under the prop roots of red mangrove where it feeds on crabs. The green- back heron is the most commonly observed wading bird at Twin Cays. It breeds on the island and builds its nest in the red mangrove fringe along the channels. It is frequently seen diving for small fish in the shallow, interior ponds.

The most conspicuous birds of the area are the brown pelican and frigate bird, which can also be seen flying overhead or perched in mangrove trees.

Only four or five reptile species are known from the Belize mangrove cays: James F. Lynch has found one species of lizard (Anolis sagrei) to be abundant on the island, but it is commonly seen in red mangrove trees. Feeding on ants, termites, and other insects. Less common is the boa constrictor (Boa), which populates most of the larger islands. The ground iguana (Cteno- saurus) and a couple of gekko species are pre- sent only on a few of the islands.

Two common land crab species occur on the islands. The mangrove tree ceb (Astrakosponi, currently under study by Kim Wilson, Central Centennial State University) moves up and down the banks and aerial roots of red mangrove. Uca cubensis, the largest land crab on the islands, lives on the ground under the dense mangrove canopy where it builds large, extensive burrows near the upper limits of the high tide. Belizean fisher- men consider the burrows of these to be the primary breeding sites for sandflies and mosqui- toes. William P. Davis (Environmental Protection Agency, Gulfstream, Florida) and D. Scott Taylor (Vero Beach, Florida) have found Uca cubensis bur- rows to be havens for the mangrove Rufus, a hermaphroditic fish.

The penknife (Utterlina angulata) is widespread on all the mangrove islands. These arbo- real snails migrate slowly between the mean high water level and the tops of red mangrove trees; they are the subject of research conducted by Lauren Sullivan, University of Ala- bama, Brad Bellout and Jan Kohlmeyer. Univer- sity of North Carolina determined that these snails are very narrow zone on the prop roots, just above the mean high-water level.

Insects are, by far, the most Species-rich and abundant group of supratidal animals inhabiting the Belizean mangrove cays. Ants, in 22 or so species, are clearly the most abundant. Termi- nates, because of their huge nests and extensive covered walkways, are the most cons-picuous. Some major groups of insects, such as bees, are poorly represented in the mangrove fauna. As in other tropical ecosystems, a large percentage of the insect species that we have found associated with mangroves is undescribed.

The surface of the salt water, the interior ponds, and the mudflats provide habitats for aquatic and semiaquatic insects, including members of five families of true bugs (Hemipte- ra) and three families of beetles (Coleoptera). Paul J. Spangier and Robin Faircloue (De- partment of Entomology, Smithsonian Institu- ion) studied this group along the similar fauna
on the mainland. The cays have fewer kinds of aquatic habitats, and a corresponding lower species diversity in this part of the insect fauna.

Wayne N. Mathis (Department of Entomology, Smithsonian Institution) found an astounding 51 species of shore flies (Ephyridae) along the margins of these mangrove islands although none of these species is endemic. Most of these species are detritivores, living on the peat-based muck or in decaying seagrass and algae that wash ashore.

The mangrove trees and mangrove associates provide numerous supralalal habitats for primary and secondary phytophagous insects as well as their parasites and predators. Because most of these species have cryptic behavior, the diversi-
ty of insects in mangroves can easily be under-estimated. The foliage of each species of mangrove supports a unique suite of leaf-eating insects, although the damage to the leaves is much more apparent than the insects themselves.

Leaves and twig terminals of red mangrove, in particular, serve as an important habitat for a diverse assemblage of insects (Fig. 4). Because vegetative growth in the canopy is thinned almost exclusively from apical buds in twig terminals, herbivore damage here is particularly important to the tree. The apical bud is commonly attacked by a moth larva (Ecydnotrophina sp.) that causes the enveloping stipules to turn black. A larva usually eats only a portion of the young, folded leaves in a bud, leaving the meristemoid tissue intact. However, sometimes the entire apical bud is destroyed as a result of this form of herbivory and any potential for further growth by the damaged twig is lost. A number of other moth larvae feed on red mangrove leaves, but because insect taxonomy is based primarily on adult specimens, identifications of these larvae are almost impossible without rearing them. Moth larvae that feed on leaf surfaces encase themselves in a variety of protective coverings, such as frass tubes or portable cases built of mangrove twigs and bark. Serpentine galleries of a leaf, twig, and propagule mining moth larva (Microlepidoptera, Gracillariidae) are also common on red mangrove, although both larval and adult specimens are rare. Adult insects that feed on these leaves are primarily nocturnal. A guide of at least six species of wood-boring insects are primary herbivores on the twigs of red mangrove. Ordinarily, each twig hosts only one individual. As it feeds, the larva hollows the twig. When the adult wood-borer emerges via an exit hole, access is provided to the hollow twig. These species are critical to many small arthropods, including ants, other insects, and spiders, that are not wood-boring and are dependent on finding suitable spaces in which to build nests or to take refuge. So far, we have found more than 70 species associated with hollow red mangrove twigs.

At least 35 species of xylaphagous (wood eating) beetles and moths have been identified from the three mangrove species. More than half of these are wood-borers in the Long-Horned Bettle family (Cerambycidae). Although some of the species are generalists, feeding on any available dead wood, a few specialist species appear adapted to a single mangrove species. Our research indicates that these arboreal wood-borers play significant roles in the mangrove ecosystem. The larval stages of these insects are the primary herbivores. They modify the trees by constructing galleries and pulp chambers in the living and dead woody tissue. These spaces are used as habitats by numerous invading arthropods, such as ants, termites, other beetles, spiders, isopods, scorpions, pseudoscorpions, scale insects, centipedes, crickets, katydids, and roaches. The infestation by wood-borers is extensive on the islands; all species of mangroves and almost every tree sampled have hosted at least one and usually several species. Wood-borers girdle, as well as hollow, mangrove stems and boles. In red mangrove, these activities frequently result in death, weakening, and subsequent pruning of all branches beyond the point of attack.

Conclusions

The red mangrove fringe, the specialized vegetation, the physical environment, and the associated fauna and flora form a complex and diverse island community above water as well as below. We have learned that mangroves produce fine sediments and organic detritus and stabilize them by modifying the wave and current regimes of the open lagoon. The diversity of species has yet to be completed, but already we have shown that morophya are represented by species of which 10 to 25 percent, and in some cryptic microscopic-sized group up to 60 percent, are undescribed. The mangrove swamp is rich in recycled nutrients and high in production rates but its occupants are severely stressed by factors such as salinity and temperature fluctuations, desiccation potential, abundance of fine sediments, and shortage of firm substrates. Space, from the sea bottom to the tree tops, is distinctly partitioned by the animals that exploit this specialized plant community. These island communities, because of their isolation from the Beleza mainland, provide us with ideal locations to study pure mangrove communities in the Caribbean.

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