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Waterweed Invasions

Vast vegetative mats of the two most noxious aquatic weeds plague the world's waterways. Investigations of the water hyacinth and the kariba weed are leading to new programs for weed control

by Spencer C. H. Barrett

Populations of plants and animals ordinarily migrate and multiply slowly over time as a result of the natural interplay among many ecological factors: soils, waters, glaciation, drought, the rise and fall of competitor species. Yet in some regions human activities have quickened the pace of change by dramatically altering the range and abundance of many species. Today plants and animals are shipped, sometimes accidentally, all over the globe to zoos and botanical gardens and for commercial and agricultural purposes. A small minority of the "alien," or introduced, species become ecological as well as economic disasters: although they may have been innocuous in their native region, these species are transformed into aggressive pests or weeds that invade and dominate their new environment.

Nowhere are these biological invasions more evident than in the rivers, lakes and reservoirs of the world. In the past century more than a dozen weed species have laid siege to the world's waterways. Canadian species, such as the pondweed *Elodea canadensis*, have infested canals in Europe. In return native European weeds, such as the Eurasian water milfoil, *Myriophyllum spicatum*, have overgrown lakes in Canada. Such native tropical species as the alligator weed, *Alternanthera philoxeroides*, have clogged irrigation systems in the U.S.; to even the score, such native American weeds as the grass *Echinochloa microstachya* have invaded rice fields in Australia.

Two species of aquatic weeds exemplify the problem such pests can create: the water hyacinth, *Eichhornia crassipes*, and the kariba weed, *Salvinia molesta*. These two species have wreaked havoc on waterways throughout the world, particularly in the tropics and subtropics, where they cause severe hardship and immense economic difficulties. In a single growing season the weeds can reduce a thriving water community to a destructive mass, halting transportation, killing fish and promoting disease.

In an attempt to eradicate the water hyacinth and the kariba weed, farmers, biologists and government officials have launched valiant weed-control programs and have spent millions of dollars on mechanical and chemical remedies. Unfortunately, most mechanical methods cannot destroy plants fast enough, and herbicide controls have harmful side effects on water quality, fish stocks and other elements of the aquatic food chain. However, new programs developed from careful studies of these noxious weeds offer hope.

The water hyacinth and the kariba weed share a feature common to most weeds: the ability to grow and multiply rapidly in habitats that are disturbed by human activity. In recent times the large-scale disruption of natural ecosystems has opened up many new ecological niches for these aquatic weeds. Irrigation schemes, hydroelectric projects and artificial lakes establish ideal environments. In natural waterways the plants prosper on a steadily replenished supply of nutrients that agricultural activities provide by the runoff of fertilizers and the leaching of minerals from soil.

Two special characteristics, high mobility and clonal propagation, have allowed the water hyacinth and the kariba weed to reign over this rich aquatic domain. Their high mobility is made possible by air-filled tissue known as aerenchyma, which gives the stems and leaves of the plants considerable buoyancy. The weeds can therefore float with wind or water currents to unoccupied waters, where they can grow and regenerate.

Clonal propagation helps the weeds to grow rapidly over large areas. Recently the word "cloning" has become a familiar term because of popular interest in molecular biology and genetics. Cloning has similar connotations in botany. Cloning in the botanical sense is the propagation of genetically identical plants by asexual reproduction from some sexually produced ancestor. A clone is therefore a plant produced without fertilization of male and female gametes; it represents an identical genetic copy of the parent plant. This kind of cloning will be familiar to anyone who has grown ornamental plants from cuttings.

The water hyacinth and the kariba weed display a particularly fascinating method of clonal propagation: the plant breaks apart into many separate pieces, each having the potential to grow into a complete organism. As wind or water currents disperse the fragments, colonies can expand rapidly over vast open stretches on the water surface. Freed from competition with other plants and guaranteed almost unlimited space, nutrients and sunlight, the water hyacinth and the kariba weed grow and multiply at an extraordinary pace to achieve some of the highest rates of biomass production recorded in the plant world. Consequently, a single genetic individual

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WATER HYACINTH, exported from its native South American region for its striking beauty, now grows uncontrollably over the world's rivers and lakes. In four months two plants can yield 1,200 offspring. The water hyacinth's growth has devastated many aquatic communities.

may be essentially immortal, covering vast areas and experiencing many different environments.

The water hyacinth is usually singled out as the aquatic weed that is most troublesome both ecologically and economically. It invades waterways at rates that have become legendary among biologists and weed-control experts. A group studying the weed in Louisiana reported that during one growing season 25 plants can produce enough biomass to cover 10,000 square meters of water surface with approximately two million plants, weighing as much as a fully loaded jumbo jet. If the plant settles in waters that are enclosed or have slow currents, colonies can coalesce to form continuous mats of living and decaying organic material as much as two meters thick.

Great green mats of water hyacinth fill reservoirs, spoiling water resources; they infest rivers, impeding navigation; they dam drainage channels, flooding lowlands; and they clog pipes, disturbing hydroelectric systems. The mats indirectly deplete the water's supply of dissolved oxygen, thereby asphyxiating fish and phytoplankton. As the weed drives fish away, it jeopardizes human nutrition in riverine communities where fish are the primary source of protein. The water hyacinth also provides an excellent microhabitat for agents of several human diseases, including malaria, encephalitis and schistosomiasis. Although the water hyacinth rarely competes with agricultural crops, it impedes the flow of water through irrigation canals and pumps and thereby hinders crop production.

The water hyacinth has spread from its native region—the tropical lowlands of South America—to more than 50 countries on five continents. In 1824 Karl Friedrich Philipp von Martius found the plant in Brazil and formally described it as *Pontederia crassipes;* later it was found to belong to the tropical genus *Eichhornia.* For the next six decades, however, the water hyacinth received little attention from botanists; apparently it was considered nothing more than a well-behaved plant. Its show of good behavior did not last for long.

Although the spread of the water hyacinth is difficult to document with complete accuracy, it appears that popular fascination with the plant began in 1884. In that year water hyacinths imported from the lower Orinoco River in Venezuela were distributed as gifts by a Japanese delegation at a cotton exposition in New Orleans. Water hyacinths have beautiful clusters of violet and yellow flowers perched atop floating rosettes of bulbous green leaves. They proved irresistible to the delegates. The botanical gifts were taken to surrounding districts and cultivated in garden ponds. They multiplied at a prodigious rate.

From the ponds the water hyacinth spread throughout the southern U.S. The plant's growth soon restricted river transportation of commodities such as corn, cotton and lumber, causing those industries to lose millions of dollars. Particularly troublesome was the 1895 invasion of the Saint Johns River in Florida: gale-force winds blew the water hyacinths up and down the river for more than 160 kilometers, creating huge floating mats as much as 40 kilometers long.

REMARKABLE SIMILARITIES between the water hyacinth, *Eichhornia crassipes* (*left*), and its docile relative, *E. azurea* (*right*), have helped botanists to single out the water hyacinth's aggressive traits. Although the roots of *E. azurea* restrict its growth to the edges of waterways, *E. crassipes* floats freely, and so the hyacinth can spread over vast stretches of water surface.

Word of the water hyacinth's beauty apparently traveled faster to Southeast Asia than news of its destructive powers. In 1894 the caretakers of the Bogor Botanical Garden in Java reported that the water hyacinth had become such a nuisance that specimens were routinely discarded into a river flowing through the gardens. Many local infestations soon followed. Today mats of water hyacinth can be found all over Southeast Asia as well as in the warm lowlands of India, Sri Lanka, China and Japan.

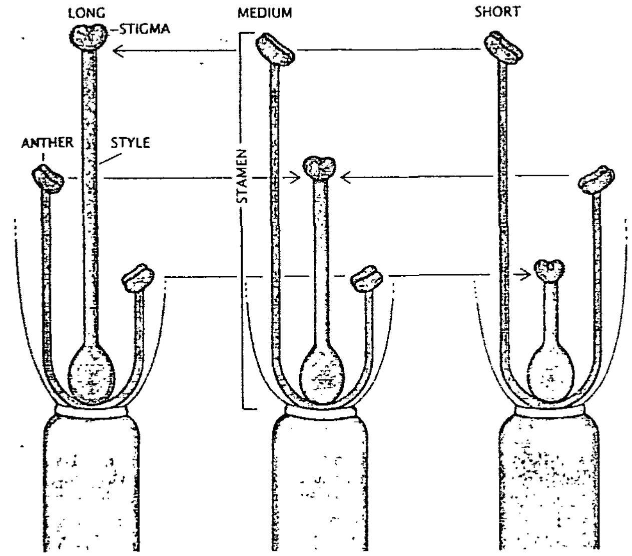
The water hyacinth has spread just as rapidly through the African continent. Boat traffic along the Congo and Nile rivers and their tributaries seems to have promoted the invasion: plants that became attached to paddle-wheel steamers sometimes hitchhiked 1,600 kilometers upstream.

As one might expect, most research on *Eichhornia crassipes* has been aimed at understanding its growth and devising ways to control it. Virtually all of this work has been done in the nonnative range of the species, particularly in the southern U.S., India and Southeast Asia.

More than a decade ago I began an investigation of *Eichhornia* in its native range. I wanted to understand more about the population biology of the remarkable *E. crassipes* and to learn something of the behavior of its little-known relatives. These studies have clarified several misconceptions about the reproductive biology of the water hyacinth and in addition have provided ecological explanations for many of its unusual reproductive characteristics.

The genus *Eichhornia* belongs to the monocotyledonous family Pontederiaceae, which includes the North American pickerelweed, *Pontederia cordata.* *E. crassipes* is one of eight species of freshwater plants in *Eichhornia.* All are native to the tropics of Central and South America, except for the African species, *E. natans.* Most species of *Eichhornia* are distributed widely throughout their native regions and regenerate by cloning. Yet *E. crassipes* is the only member of *Eichhornia* that has shown any tendency to become a noxious, aggressive weed.

That fact is particularly puzzling when one considers that the morphology of *E. crassipes* is quite similar to that of *E. azurea.* Both species form floating mats and produce large, showy flowers. More significant, *E. azurea,* like *E. crassipes,* has been exported from South America to decorate ponds and has occasionally escaped into local aquatic environments. Yet *E. azurea* has never become a serious weed problem. What makes *E. azurea* just another ornamental pondweed and *E. crassipes* the world's most aggressive aquatic weed?



CHARLES DARWIN studied the reproductive organs of morphs, or forms, of *E. crassipes* that have long and medium styles and deduced the existence of a short-style morph. He observed that the anthers of the long stamens of the medium-style morph corresponded to the stigma of the long style and that the anthers of the medium stamens of the long-style morph corresponded to the stigma of the medium style. However, the short stamens of the long- and medium-style morphs did not have sexual partners. Darwin therefore predicted that there must be a third floral morph that had not yet been discovered. The author found the short-style morph in 1974.

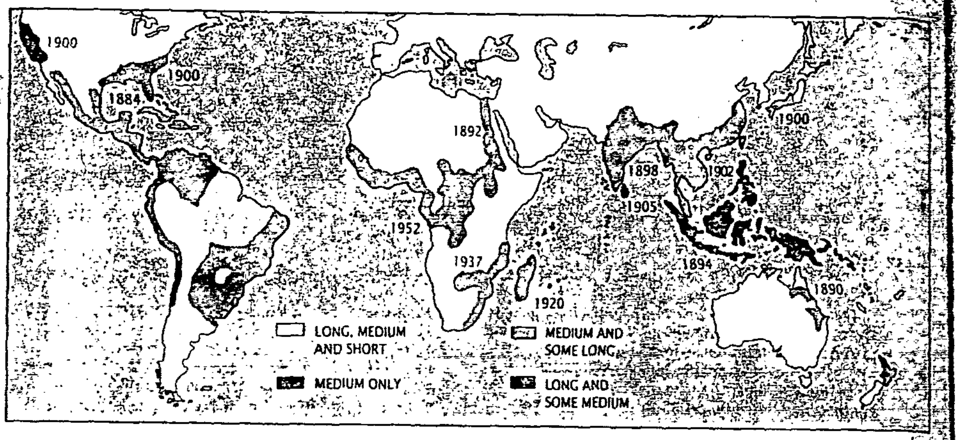
The answer lies primarily in their differing abilities to fragment into pieces that develop into whole individuals. *E. crassipes* breaks apart more readily because its rosettes of floating leaves are held together only by delicate horizontal stems called stolons. *E. azurea,* on the other hand, regenerates more slowly; its colonies cannot grow rapidly unless the plants are rooted firmly to the mud bottom. The roots of *E. azurea* restrict its distribution to shallow ponds and the edges of lakes and rivers. In contrast, because *E. crassipes* floats freely, it can grow and multiply on the surface of deep waters, away from most competitors.

Why has *E. crassipes* evolved the ability to float freely and fragment rapidly? The answer lies in the ecological conditions and habitats that *E. crassipes* occupies in its native region.

The two areas where the water hyacinth is thought to have originated are the Amazon basin and the extensive lakes and marshes of the Pantanal region in western Brazil. The two regions provide a dynamic aquatic habitat. Water levels of local lakes and rivers fluctuate dramatically because of seasonal changes in rainfall. The waters of the Amazon River, for example, rise and fall about 10 meters annually, even as far as 2,000 kilometers upstream from the Atlantic Ocean. Under these conditions the free-floating habit is highly adaptive, whereas rooted plants often perish during periods of submersion in deep, muddy water.

The Amazon basin and the Pantanal also contain many shallow, interconnected, nutrient-rich lakes and pools created by annual floods. These seasonal lakes provide ideal conditions for the explosive growth of water hyacinth. If a small colony of *E. crassipes* finds itself stranded in a lake after a flood, it proliferates by absorbing the abundant resources.

Ecological studies in the native region led me to another interesting finding. *E. crassipes* produces a great



FLORAL MORPHS with long, medium and short styles have spread over five continents in a curious distribution. The three floral morphs grow together only in the water hyacinth's native region, the lowland tropics of South America. The dates on the map show when, according to historical records, the water hyacinth was introduced to a particular region.

number of seeds that can survive dry spells. The seeds help to regenerate populations after the desiccation of colonies. This observation and others laid a common misconception to rest. Many investigators assumed that clones of the water hyacinth were sexually sterile and could not regenerate from seed. This assumption was largely based on two generalizations. First, plants that grow exclusively by vegetative propagation over long periods (such as sweet potato, sugar cane and many ornamental plants) often lose their ability to reproduce sexually: genetic mutations that impair pollen and seed fertility tend to accumulate over time. (Mutations of this type are continuously eliminated from the gene pool of species that reproduce sexually in regular cycles.)

The second generalization that suggested sterility was based on misconceptions about the water hyacinth's breeding system. Flowers of *E. crassipes* can be divided into three sexual types that differ in the length and position of their reproductive organs, the male stamens and the female pistil. These types, or floral morphs, are distinguished by their long, medium or short styles—prolongations of the ovary. Hence, *E. crassipes* is described as tristylous.

Tristylous plants are usually self-incompatible and intramorph-incompatible. In other words, very few seeds are produced as a result of self-pollination and pollination by other plants of the same morph. (Crosses between flowers of different morphs yield many seeds.) The theory that heterostylous flowers are self-incompatible and intramorph-incompatible came from Charles Darwin. He first investigated the floral morphology and breeding relationships of heterostylous plants. In 1877 he published his findings in *Different Forms of Flowers on Plants of the Same Species*. Because of the self-incompatibility of the water hyacinth, many botanists believed it would produce few seeds in regions where one style morph grows, as is the case in most areas.

Yet my own experiments indicate that high levels of seed fertility are achieved in many single-morph colonies of *E. crassipes*. I found that individual clones are self-fertile and intramorph-fertile. In fact, most clones can produce thousands of viable seeds.

The failure to recognize that many seeds are often produced in water hyacinth populations has complicated weed-control efforts. One technique, still employed in various parts of the world, involves the drainage of water from infested canals and reservoirs during certain periods of the year. This practice, known in the U.S. as drawdown, destroys the vegetative parts of aquatic plants through desiccation. Yet drawdowns also provide excellent opportunities for weeds to germinate and establish seedlings: they remove the leaves of floating mats that usually shade seedlings, and they establish moist sediments, in essence mimicking the water-level fluctuations of the Amazonian habitat.

Although the water hyacinth was an exception to Darwin's findings that heterostylous plants are usually self-incompatible, he proved correct about other features of the plant. Darwin received dried flowering specimens of *E. crassipes* from southern Brazil. He identified the flowers as examples of the long- and medium-style morphs. He then deduced that there should also be a short-style morph because both the long- and medium-style morphs had short stamens. Darwin's deduction later sparked considerable controversy, but no definitive evidence was found to prove that the short-style morph existed.

In the 1950's, in an effort to find the missing form, the geneticist J.B.S. Haldane enlisted the help of schoolchildren in India to survey populations of water hyacinth. This effort and many others failed. By the early 1970's botanists had reached the conclusion that the short-style morph was extinct and that *E. crassipes* had two floral forms, not three.

I was aware of this controversy in 1974, when I began working in the lower Amazon basin of Brazil. There I encountered my first flowering colony of water hyacinth growing in marshes associated with the river Jari. The flowers had short styles! Darwin's deduction was confirmed.

Later I conducted a more extensive geographic survey of the morphs of

water hyacinth in North and South America with Wendy Forno of the Commonwealth Scientific and Industrial Research Organization (CSIRO) in Queensland, Australia. We found that the short-style morph has a more restricted distribution than the long- and medium-style morphs have [*see illustration on opposite page*]. The short form grows primarily in the Amazon basin and the Pantanal, and it has been sighted in the Paraguay and Paraná rivers. From a global perspective the medium-style morph predominates throughout the nonnative range; the long-style morph occurs less frequently. What factors account for this curious geographic pattern of style morph distribution?

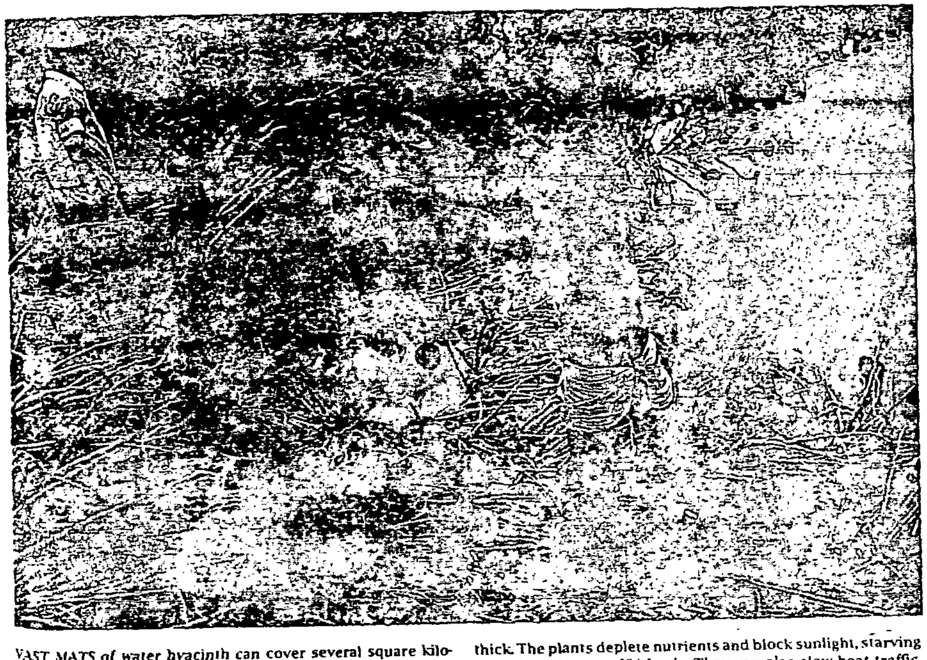
Although the short-style floral morph grows as rapidly and floats as freely as the other morphs, it is confined to parts of South America probably because of its relationship with a local pollinator. Several different types of bees visit the large flowers of the water hyacinth to feed on pollen and nectar. Most of them contact the stigma (the pollen receptor) at the tip of the long and medium styles and thereby mediate pollination. The narrow flower of the water hyacinth conceals the stigma at the tip of the short style from most pollinators, however. The long-tongued bee *Ancyloscelis gigas* is the only known pollinator that can easily contact the stigma of the short-style morph, and that may account for the restricted range of the short-style morph. The fact that the short-style morph is absent from the Old World range appears to be simply the result of chance. The short-style morph has not been exported to other regions.

The geographic distribution of style morphs reflects a principle introduced by the evolutionary biologist Ernst Mayr of Harvard University: a new population that is started by a few individuals displays less genetic variation than does the parent population. Hence, if a few clones are isolated from their ancestral gene pool and inaugurate a new population, they can give rise to genetically uniform populations. Just such a sequence of events appears to have happened many times during the spread of the water hyacinth.

Most populations in the nonnative range are composed of the medium-style morph. Historical record and geographic distribution seem to imply that many invasions may have originated in Venezuela, where that morph predominates. The fact that the long-style morph appears periodically (albeit infrequently) in the nonnative region does not necessarily mean that it was introduced separately. A population of medium-style morphs can give rise to long-style morphs because of the pattern of inheritance of tristyly.

In the water hyacinth two genes determine the length of the style. One gene controls whether or not the style will be short. If the short trait is not expressed, a second gene controls whether the style is medium or long. The second gene has two alleles, dominant (M) and recessive (m). If a plant is homozygous for m (both of its copies of the gene are recessive), its flowers will have a long style. If a plant has at least one copy of the dominant gene (it is mM or Mm or MM), its flowers will have a medium style.

In heterozygous plants the pollen and ovules, each of which carries a copy of the gene, can have either form, dominant (M) or recessive (m). When the forms combine during sexual reproduction, the gene complement of the offspring has one chance in four of being homozygous for a dominant



VAST MATS of water hyacinth can cover several square kilometers of water surface and can grow as much as two meters thick. The plants deplete nutrients and block sunlight, starving out other plants and animals. They can also slow boat traffic.

medium-style gene (*MM*), two chances of being heterozygous for the dominant gene (*mM* or *Mm*) and one chance of being homozygous for the recessive gene (*mm*)—and of having a long style. In a population of medium-style morphs that are heterozygous, then, about one fourth of the offspring of sexual reproduction will have flowers with long styles. If a few long-style plants appear in populations that mainly have medium-style plants, one can assume that the population probably reproduces sexually, which in turn indicates that its environment allows seeds to germinate and seedlings to grow.

In California, where only medium-style plants occur, seeds were collected and segregated to grow long-style plants in a greenhouse. The absence of the long-style morph in California, then, indicates that the water hyacinth probably does not reproduce sexually under the ecological conditions typically found in the state. It is also possible that populations in California originate from one or a few clones that have propagated vegetatively since the beginning of the century. Many other regions of the introduced range also exhibit this genetic uniformity.

Botanists hope to exploit genetic uniformity as a way to control the water hyacinth. For a time, it was believed that the tropical sea cows called manatees could be introduced into regions to feed on the water hyacinth and thus control its growth. This program was successful in Guyana. In other areas, however, researchers discovered that the manatee does not find the water hyacinth very tasty and often prefers other vegetation to it.

Although the results of programs for eradicating the water hyacinth have been disappointing, success has been achieved in controlling the world's second most troublesome aquatic plant, the kariba weed, *Salvinia molesta*. This curious free-floating fern is so tiny and delicate that most people are surprised to learn that it is an aggressive invader.

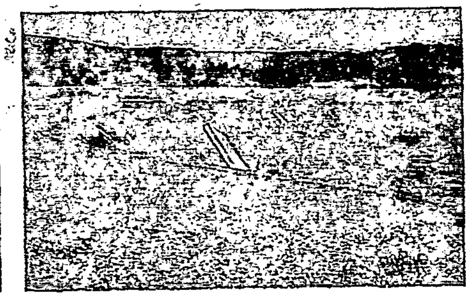
The kariba weed forms mats about one meter thick and spreads out over water surfaces in a way similar to the water hyacinth. Under favorable conditions the kariba weed can double its biomass in as little as 2.2 days—five times faster than the water hyacinth.

In the past 50 years the explosive growth of *S. molesta* has had an adverse socioeconomic effect in parts of Africa, Asia and Australia. A notable invasion took place at Lake Kariba on the Zambezi River in Africa, where at its peak in 1962 the weed covered 1,000 square kilometers, nearly one quarter of the total area of what was then the world's largest reservoir. The infestation earned the plant a common name, the "kariba" weed.

Nowhere has the plant had more of an impact than in the floodplains of the Sepik River in Papua New Guinea, north of Australia. After its introduction in the early 1970's, a colony of kariba weed covered all the lakes in the lower half of the floodplain, a total of 250 square kilometers of water surface. The invasion threatened the lives of 80,000 people who depend on the river for food and transportation.

The kariba weed had been identified as *Salvinia auriculata*, a native of South America, until the 1970's. In 1972 David S. Mitchell of CSIRO in New South Wales located a herbarium specimen of *S. auriculata*. The specimen had been discovered in 1941 along with two other related species. All three specimens originated from the botanical garden in Rio de Janeiro. Botanists began to suspect that the kariba weed was a horticultural hybrid, an offspring of the two related species from the garden. The fact that the kariba weed was sterile seemed to confirm the plant's hybrid origin.

MANATEE, commonly known as the tropical sea cow, munches away on water hyacinth in Blue Spring State Park in Orange City, Fla. The manatee has been introduced into tropical waterways to help control the rapid spread of water hyacinth.



DELICATE LEAVES of the kariba weed, *Salvinia molesta* (*left*), belong to a single genetic individual that blankets waterways around the globe. The weed is perhaps the most massive entity in the botanical world. A floating mat of it is shown at the right.

Later Mitchell described the kariba weed as a new species and named it *Salvinia molesta*, the epithet signifying its aggressive nature. In 1978 the CSIRO team of Forno and K. L. S. Harley at last discovered the native range of *S. molesta* in southeastern Brazil and cast doubt on the original theory that the plant was an artificial hybrid.

Although it now seems unlikely that *S. molesta* originated in a botanical garden, its characteristic hybrid vigor is undoubtedly one of the secrets of the plant's extraordinary behavior. Hybrid plants often grow rapidly and are usually sterile. This is the case for *S. molesta*. In contrast to the water hyacinth, which can reproduce sexually, *S. molesta* propagates entirely by clonal means.

The fact that *S. molesta* is asexual means that the world's entire population of the plant may be a single genetic individual. Because many millions of tons of the weed are distributed around the world, from a genetic viewpoint *S. molesta* may lay claim to being the largest individual organism on the earth.

The aggressive behavior of the kariba weed has largely been displayed outside its native South American range. This is true in the case of most biological invasions. Plants and animals usually populate their native environments at densities commensurate with their ecological role in a balanced community, but when species are introduced to another part of the world, they leave behind the co-evolved competitors and enemies that normally keep their populations in check. The absence of natural enemies in the nonnative range allows alien populations to increase rapidly and leads to "ecological release."

Knowledge of the causes behind the different behaviors of species in their native and introduced ranges has led to novel methods of managing pest and weed outbreaks. These methods, known as biological control, reduce population numbers to acceptable levels through the planned release of host-specific natural enemies.

Biological control of the kariba weed was initiated shortly after botanists located its native range. While exploring the plant's Brazilian homeland, Forno, P. M. Room and P. A. Thomas of CSIRO in Queensland discovered a new beetle species that feeds exclusively on *S. molesta*. (The beetle was later named *Cyrtobagous salviniae*.) Their work is the most successful example so far of biological control of an aquatic weed.

The beetle was brought to Australia and released at Lake Moondarra, where it rapidly destroyed an infestation of kariba weed covering two square kilometers. The beetle's most spectacular success was achieved in Papua New Guinea, where between 1983 and 1985 the weed cover was reduced from about 250 square kilometers to two square kilometers. It was estimated that the beetles consumed two million metric tons of the weed in just two years. Other beetle programs are now under way in India and Namibia and are rapidly achieving control.

Although biological control is not a universal solution to all pest and weed problems, the technique may be applied to many other waterweed invasions. A survey conducted by Jeremy J. Burdon and Don Marshall of CSIRO in Canberra examined 81 attempts to control 45 weed species. They found a correlation between the level of control and the reproductive system. Asexual species were controlled much more effectively than those that rely on sexual reproduction.

Presumably biological control succeeds if genetic variation is limited. If this assumption is true, the water hyacinth and many other aquatic weeds that regenerate primarily by clonal means should be excellent targets for biological control. Clonal propagation, which allows water hyacinth and kariba weed to dominate the world's waterways, may yet provide a way to sink these noxious invaders.

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